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UNIVERSITY OF ALBERTA

SYSTEMATIC STUDY OF THE FAMILY CREEDIIDAE (PERCIFORMES : TRACHINOIDEI)

BY

Ierecê Maria de Lucena Rosa

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

DEPARTMENT OF ZOOLOGY

Edmonton, Alberta
Spring, 1993

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled SYSTEMATIC STUDY OF THE FAMILY CREEDIIDAE (PERCIFORMES : TRACHINOIDEI) submitted by IERECE MARIA DE LUCENA ROSA in partial fulfillment for the degree of Doctor of Philosophy.

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This thesis is dedicated to my daughter Carolina.

ABSTRACT

The family Creediidae is a phenotypically distinct group, consisting of seven genera of marine fishes, mostly found in shallow waters in the Indo-Pacific Ocean. This thesis presents a systematic study of the Creediidae and its included taxa, with the following main objectives: 1) to determine the validity of the nominal species; 2) to provide diagnoses for the family and its included taxa; 3) to provide detailed, comparative species descriptions; 4) to describe and compare osteological characters for all creediid genera; 5) to establish monophyly for the family and genera; 6) to examine interfamilial relationships.

All species previously assigned to the Creediidae are taxonomically reviewed. Of the sixteen nominal species, fourteen are recognized as valid. Chalixodytes chamaleontoculis Smith, 1956 and Chalixodytes tauensis Schultz, 1943 are conspecific, and therefore their names are synonomyzed. Limnichthys donaldsoni is synonymized with Limmichthys nitidus.

A data matrix consisting of 77 unweighted, unordered characters was produced. Data were analysed using PAUP version 3.0S. A single minimum length cladogram (109 steps, 0.78 C.I., excluding uninformative characters) was generated, both by the heuristic and Branch-and-Bound search options. Monophyly of the Creediidae is demonstrated by several synapomorphies, such as: pelvis cup-shaped, ventral surface of upper end of cleithrum with spine and gill rakers confined to the lower limb of branchial arch.

Creedia Ogilby and Schizochirus Waite are hypothesized to form and monophyletic group, sister-taxon to the other creediids. The remaining creediids form a monophyletic group, based on a number of synapomorphies, such as: round second infraorbital and no postcleithrum. Limnichthys Waite and Tewara Griffin share two synapomorphies and may form a monophyletic group. Crystallodytes Fowler, Chalixodytes Schultz and

Apodocreedia de Beaufort constitute a monophyletic group, based on three synopomorphies. Apodocreedia de Beaufort and Chalixodytes Schultz share one synopomorphy and may form a monophyletic group.

Creedidae, Trichonotidae and Percophidae (at least Hermerocoetinae) form a monophyletic group based on six synapomorphies. Sister-group relationship for the Creediidae apparently lies within the Hemerocoetinae, but that hypothesis is very provisional and should be re-examined once the Percophidae becomes better defined.

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I. INTRODUCTION

The family Creediidae presently includes seven genera and 16 nominal species of marine fishes commonly known, due to their burrowing habits, as sandburrowers. They are small, reaching a maximum length of 86 mm. Creediids occur in tropical and subtropical areas of the Indian and Pacific oceans, mostly in shallow water, over sandy or gravel bottoms. Three of the creedid genera, Schizochirus, Apodocreedia and Tewara, are respectively, restricted to Australia, Southeast Africa and New Zealand. Creedia is found primarily in Australia but one of its species occurs in Japan; Crystallodytes is distributed in the Central Pacific and Easter Island. The two remaining genera, Limnichthys and Chalixodytes are widely distributed in the Indo-West Pacific.

Members of the family are easily recognized by having a fleshy tip on the upper jaw which extends beyond the lower jaw (see Fig. 1), cirri bordering the lower jaw, lateral line (at least posteriorly) running near the ventral profile, and lateral line scales with a posteriorly expanded central lobe.

Creediid fishes have been the object of a few systematic studies in recent years (Nelson, 1978, 1985), but most of the literature on the group consists of short redescriptions or citations of their occurrence in a particular geographic area. Further work is necessary at all taxonomic levels within the group. For instance, there are uncertainties regarding the number of species that should be placed in the genera Limnichthys and Chalixodytes; the interrelationships of the creedid genera have only been partially examined (see Nelson, 1985) and the intrafamilial relationships are still unresolved (see Nelson, 1985; Pietsch, 1989).

The main objectives of this study are: (1) to provide diagnoses for the family Creediidae and for its included taxa; (2) to determine the validity of the nominal species; (3) to provide detailed, comparative species descriptions; (4) to describe and compare osteological characters for all creediid genera; (5) to establish monophyly for the family and genera; (6) to examine interfamilial relationships.

II. HISTORICAL REVIEW

II.1. FAMILY CREEDIIDAE

The taxonomic history of the creediid fishes begins with the description of Hemerocoetes haswelli Ramsay, 1881, originally described as part of the family Trichonotidae. The placement of that species in Hemerocoetes was by no means certain, as expressed by Ramsay himself: "I have placed this fish provisionally in the genus Hemerocoetes to which it comes nearest, it is not however identical with that genus".

Later, Ogilby (1898) established the genus Creedia for the new species C. clathrisquamis, but was unable to assign it to any known family, treating it as an incertae sedis taxon. Waite (1899), recognizing that Creedia comprised a family of its own, erected the Creediadae (emended to Creediidae); later, he (Waite, 1904a) synonymized Hemerocoetes haswelli and Creedia clathrisquamis, and indicated that the correct designation for the taxon should be Creedia haswelli. In the same year, Waite (1904b;c) described two other genera, Limnichthys and Schizochirus, which he assigned to the family Trichonotidae. Waite (1904c) pointed out that the two genera were closely allied, and that Creedia, the once sole member of his family Creediidae, perhaps should be placed in the Trichonotidae. Also, Waite's uncertainty regarding the limits between creediids and trichonotids persisted among subsequent authors, and as shown below, only recently were the two families diagnosed on the basis of both external and osteological features.

Regan (1913) treated the Creediidae as a valid family, and established a new family, Limnichthyidae, for Limnichthys and Schizochirus. Regan's scheme was accepted by Jordan (1923) and Berg (1940) and remained virtually unchanged (except for the inclusion

of Squamicreedia in the Creediidae, by McCulloch, 1929), until Schultz (1943).

Schultz, in an attempt to classify the genera referred to the Trichonotidae at various times, divided the family into four subfamilies: Limnichthyinae, Trichonotinae, Kraemerinae and Paragobioidinae. Creedia and the other five genera were placed in the Trichonotinae; the Limnichthyinae was an expansion of Regan's (1913) Limnichthyidae: 1) genera Limnichthys and Schizochirus, traditionally placed in that taxon, were maintained in the subfamily; 2) two genera described after Regan's paper, Tewara and Crystallodytes, were incorporated to that assemblage, and 3) a new genus, Chalixodytes, was also placed in the Limnichthyinae. Aside from the fact that Schultz, like Regan, did not include Creedia in that assemblage, the composition of his Limnichthyinae closely resembles what is presently known as family Creediidae.

Subsequently, Schultz (in Schultz et al., 1960) presented a different scheme for the "genera related to the Trichonotidae and Percophididae": he no longer grouped them into subfamilies and all genera currently recognized in the family Creediidae (plus another seven genera) were included in the family Trichonotidae.

Later workers (e.g. Greenwood et al., 1966; Nelson, 1976) recognized the Trichonotidae, Creediidae and Limnichthyidae as separate families. Nelson (1978), however, after examining most species placed either in the Creediidae or Limnichthyidae, proposed that the two families should be combined, the name Creediidae having priority over Limnichthyidae. In subsequent publications, Nelson (1978, 1983) and Nelson and Randall (1985) described four new Creediidae species, bringing their number to 16. Nelson (1979, 1985) compared various species of Creediidae on the basis of their osteological features, considerably improving the delimitation of the family. A summary of the various classifications proposed for creediids is given in Table 1.

II.2. TRACHINOID FISHES

The family Creediidae has been traditionally placed among "Trachinoid fishes", a group initially proposed by Günther (1860) as Family Trachinidae (see Pietsch, 1989, for a historical account of trachinoids). Trachinoid families have been combined in distinct ways by different authors, but not clearly defined. This has rendered selection of outgroups and interpretation of character distribution, both within and among families, difficult. Nelson (1984), in one of the most recent proposals for the group, pointed out problems regarding the placement of some families in that assemblage. Watson et al. (1984) indicated that "the Trachinoidea is a very diverse, probably polyphyletic group."

In the most recent proposal, Pietsch (1989), based on a cladistic analysis, recognized 10 families in the Suborder Trachinoidei. He used two characters to define that assemblage: pectoral radials small and pelvic spur present. Later, Pietsch and Zabetian (1990) pointed out that those families represent the core of, but do not necessarily delimit the Suborder Trachinoidei (in the same paper, they added the family Ammodytidae to that group). Although Pietsch's 1989 paper significantly improved our knowledge of trachinoid classification, much remains to be done. For instance, detailed osteological descriptions are still lacking for some of the so-called trachinoid families; monophyly of the suborder Trachinoidei and some of its members has not been clearly established. The distribution of the character "pelvic spur present" should be reviewed, as the spur can also be found in families Opistognathidae (a member of the Percoidei, sensu Johnson, 1984 and excluded from the Trachinoidei in Pietsch's 1989 paper), and some notothenioids (pers. obs.).

II.3. INTERRELATIONSHIPS OF CREEDIIDAE

The family Creediidae has been associated with trichonotids and/or percophids by various authors, e.g. Waite (1881), Regan (1913), Schultz in Schultz et al. (1960). However, grouping of these taxa usually lacked justification or was based on the fact that creediids, trichonotids and percophids externally resemble one another. Only recently, Nelson (1985, 1986) presented some comparative osteological data for the families Creediidae and Trichonotidae (limited osteological data for some creediids can be found in Regan, 1913 and Gosline, 1963, 1968) and provided the first evidence that the two families (and, at least Hemerocoetes) shared some derived characters (in the mesopterygoid and ectopterygoid bones). Nelson's 1986 paper suggested a "relatively close relationship between Creediidae and Trichonotidae", and the existence of "a character-complex, apparently derived, which is shared in at least creediids, trichonotids, and Hemerocoetes (and probably in other percophids)."

Pietsch (1989), based on the characters indicated by Nelson (1985, 1986), provisionally treated the Percophidae, Trichonotidae and Creediidae as a monophyletic group, but could not decide which taxon represented the closest relative of the Creediidae. Nelson (1986) and Pietsch (1989), however, indicated that the hypothesis of relationship between Creediidae, Trichonotidae and Percophidae required further testing.

III. MATERIAL AND METHODS

III.1. MATERIAL

Specimens of the 16 nominal species of Creediidae were examined and are listed under species descriptions. Representatives of the families Percophidae (subfamily Hemerocoetinae), Trichonotidae, Pinguipedidae, Champsodontidae, Bovichthyidae, Chiasmodontidae, Cheimarrichthyidae, Nototheniidae, Notograptidae, Malacanthidae, Opistognathidae and Bathymasteridae were examined to provide an initial idea of character distribution both within and outside the suborder Trachinoidei (sensu Pietsch, 1989). From those, species from four families were selected as functional outgroups: Pinguipedidae, Percophidae (subfamily Hemerocoetinae), Trichonotidae and Champsodontidae (see "Methods"). These species are listed in Appendix 1. Institutional abbreviations are presented as in Leviton et al. (1985).

III.2. METHODS

III.2.1. TAXONOMY

Systematic studies, both at the microtaxonomic and macrotaxonomic level, seek an interpretation of patterns of ancestry and descent. Species are the units upon which evolution operates, and therefore are relevant to our understanding of evolutionary processes. As pointed out by Eldredge and Cracraft (1980) "genetic and phenotypic heritable change assumes evolutionary importance (persistence in time) only to the extent that the reproductive community and its descendants persist. For organisms among which there is at least occasional sexual reproduction, this unit would conform to the reproductive concept of species. We are led to the ineluctable conclusion that species, when conceived as

reproductive units, are the units of evolution". It is, therefore, pertinent in systematic studies to indicate the criteria that have been used to define species.

Several "species concepts" have been proposed over the years, and the question "which definition should be used" has provided ground for many discussions and published material. Eldredge and Cracraft (1980), Wiley (1981), Mayr and Ashlock (1991), among others, discuss the various species concepts.

The Biological Species Concept (B.S.C.) has been widely used in various disciplines (Mayr and Ashlock, 1991). It has been criticized for being impractical or for "inferring biological characteristics for species only known from phenotypical evidence" (see Wiley, 1981). However, as mentioned in Wiley (1981), the latter point of criticism is a strength, rather than a weakness of that concept, because "the inference that a phenetic cluster is a biological species can be viewed as a prediction that stands or falls with increased data". In the present study, the postulates of the B.S.C. have been used as the conceptual framework for species recognition. Interbreeding or its absence cannot be directly tested in preserved specimens. However, this should not prevent the use of the B.S.C. in taxonomic studies. In such cases, morphological evidence can be used as an indicator of reproductive isolation (Mayr and Ashlock, 1991). Consistent morphological features for a given cluster of specimens (which may represent an autapomophy or a character or a set of characters which clearly diagnose that cluster) can be interpreted as an indication that they are reproductively isolated from specimens belonging to other clusters.

Eleven of the 16 nominal creediid species can be readily diagnosed on the basis of their external structural or osteological features; for each of those species, all the specimens examined could be grouped among themselves, some by using meristic counts alone. Each of those diagnosable clusters was considered to be a valid species.

On the other hand, four nominal species, two of the genus Limnichthys (L. fasciatus, and L. donaldsoni) and the two species of Chalixodytes (C. tauensis and C. chamaleontoculis) could not be separated by the aforementioned criterion. For those species, a Principal Components Analysis (P.C.A.) was performed, using a combination of characters, treated as two separate datasets: log-transformed morphometric variables and meristic counts (including three attributes, color pattern, number of epurals and shape of the pelvic spur) for Limnichthys species, and all but the number of epurals and shape of the pelvic spur for Chalixodytes species. P.C.A. was chosen because it does not require a priori assigning of specimens to a particular group. A correlation matrix of characters was generated by using the Statview SE+Graphics™ program on a Macintosh computer; principal components were computed from the matrix, and their scores plotted in scatter plots.

Discrete clusters, which did not show any overlap with other clusters, were considered to represent valid species.

The results of the P.C.A. are discussed under the descriptions of the pertinent species and shown in Figs. 6 -10.

Counts and measurements followed the recommendations of Hubbs and Lagler (1958), with the addition of the following measurements: opercular length, measured from the anterior margin of the opercle to the farthest tip of the opercular membrane, and preanal length, measured from the anteriormost point of the snout to the base of the first anal ray. Specimens were examined with a Wild M5 stereomicroscope and measured with calipers. Measurements are expressed as hundredths (%) of standard length.

A total of 18 morphometric and five meristic counts were taken (those marked by an asterisk were not used in the P.C.A.): total length (TL)*, standard length (SL), head length (HL), snout length (SNL), eye diameter (ED), fleshy interorbital distance (IDF)*, bony interorbital distance (IDB), postorbital length (POL), length of upper jaw (MXL), opercular

length (OPL), predorsal length (PDL), preanal length (PAL), pectoral fin length (PCL), pelvic fin length (PVL), body depth (BD), caudal peduncle depth (CPL), dorsal fin length (DFL), anal fin length (AFL), number of dorsal fin rays (DFF), number of anal fin rays (AFF), number of lateral line scales (LLS), number of pectoral fin rays, including splint-like uppermost ray (PCF)*, pelvic fin formula (PVSR)*. Mean, standard deviation, and range have been estimated for the morphometric and meristic variables, by using the program Excel version 3.0 on a Macintosh computer.

Osteological characters were obtained mainly from cleared and stained specimens (Taylor and Van Dyke, 1985); not all specimens were cleared and stained by the author, and, in some cases, they had only been stained for bone. Because of the limited number of cleared and stained specimens available for some species, radiographs, taken by using a "Torrex 150 Radiographic - Fluoroscopic System" X-ray machine were also used. Drawings were prepared with the aid of a drawing tube attached to a Wild M5 stereomicroscope. Osteological nomenclature follows Rojo (1991). The osteological description follows the style used for the Uranoscopidae by Pietsch (1989). The following abbreviations are used for the osteological characters:

AFR	Anal fin ray
An	Angular
APt	Anal fin pterygiophore
Ar	Articular
APP	Ascending process of premaxilla
Bh	Basihyal
Bo	Basioccipital
Br	Branchiostegal rays
C1-5	Ceratobranchials 1-5

Ch	Ceratohyal
Cl	Cleithrum
Co	Coracoid
CV	Caudal vertebra
D	Dentary
DFR	Dorsal fin ray
DPt	Dorsal fin pterygiophore
Ect	Ectopterygoid
E1-4	Epibranchials 1-4
Epi	Epiotic
Ep1-2	Epurals 1-2
ER	Epipleural Ribs
Ex	Exoccipital
Es	Extrascapular
F	Frontal
H1-3	Hypobranchials 1-3
Hh	Hypohyals
Hp	Hypurals
HS	Haemal spine
Hyo	Hyomandibular
I2-4	Infraorbitals 2-4
Ih	Interhyal
In	Intercalar
Io	Interopercle
L	Lacrymal
LE	Lateral ethmoid

Me	Mesethmoid
Ms	Mesopterygoid
Mt	Metapterygoid
Mx	Maxilla
N	Nasal
NS	Neural spine
O	Opercle
P 2, 3, 4	Pharyngobranchials 2, 3 and 4
Pa	Parietal
Pal	Palatine
Pas	Parasphenoid
PcR	Pectoral radials
PcV	Precaudal vertebra
Pmx	Premaxilla
Po	Preopercle
PPP	Postmaxillary process of premaxilla
Pr	Prootic
PSp	Pelvic spur
Pt	Pterotic
Ptt	Posttemporal
PvR	Pelvic fin rays
PvS	Pelvic fin spine
Q	Quadrate
Sc	Scapula
Scl	Supracleithrum
So	Subopercle

Soc	Supraoccipital
Sp	Sphenotic
Sym	Symplectic
Uh	Urohyal
Vom	Vomer

III.2.2. PHYLOGENY

The approach used to establish the relationships is phylogenetic (sensu Hennig, 1966), as outlined by Wiley (1981), also referred to as cladistic analysis. Taxa are grouped on the basis of shared derived charaters or synapomorphies, in order to reconstruct common ancestry relationships (Wiley et al., 1991).

As stated above, a central concept of cladistic methodology is the identification of synapomorphies, which will define monophyletic (natural) groups. Characters and their various states are identified and once they have been scored for all taxa under study, their polarity (plesiomorphic or primitive vs. apomorphic or derived) must be determined to reconstruct phylogeny. In my study, polarization of characters was done by the outgroup comparison method, as summarized by Maddison et al. (1984).The results of the phylogenetic analysis are depicted in branching diagrams, termed cladograms.

Outgroups were chosen based on information gathered from the literature (Nelson, 1985, 1986; Pietsch, 1989). Representatives of the Trichonotidae, Percophidae (subfamily Hemerocoetinae), Pinguipedidae and Champsodontidae have been used as outgroups. The Pinguipedidae was chosen because of its basal position among trachinoid fishes, as proposed by Pietsch (1989) or blennioids [in part], as used by Gosline (1968); the

Champsodontidae was chosen due to its postion relative to the Percophidae-Trichonotidae-Creediidae trichotomy in Pietsch's cladogram. The choice of the Percophidae and the Trichonotidae was based on the fact that the two families have been treated as closely related to the Creediidae since the latter family was established, and because in Pietsch's 1989 cladogram, the three families are shown as an unresolved trichotomy.

A data matrix, consisting of 77 characters, was constructed and run in the Phylogenetic program PAUP (Phylogenetic Analysis Using Parsimony) version 3.0s (Swofford, 1991). PAUP has been largely used in systematic studies in recent years. It is a versatile program, which contains a number of options regarding characters, minimum length trees search methods, consensus methods, etc. In the present study, minimum length trees were obtained, as suggested by Swofford (1991), first by using the heuristic search option (branch swapping option) and then by the branch-and-bound method. This was done to get an initial idea on the trees' minimum length, which can subsequently reduce the amount of time required to run the program. Heuristic searches require less computing time, but are not guaranteed to find all the minimum length trees, something that can be achieved by the branch-and-bound method. The exaustive search option was not used, as it is not feasible when more than ten taxa are involved (Swofford, 1991). Characters were entered the data matrix as unweighted and unordered. Both binary and multistate coding have been used ito construct the matrix. The data matrix was also run in the MacClade 2.1 and 2.96c versions (Maddison and Maddison, 1987, 1989), and the resulting cladogram was transported to the graphics program Superpaint 2.0.

The obtained minimum length tree (herein termed minimum length cladogram, for reasons explained in the phylogenetic analysis section) is presented in Fig. 11.

IV. FAMILY CREEDIIDAE

IV.1. FAMILY SYNONYMY

The following synonymy includes not only sensu strictu synonyms, but also suprageneric taxa in which creediids have been placed at various times.

Most creediid species have been treated, by different authors, as part of the Trichonotidae and I therefore include the latter family in the synonymy. The Limnichthyinae, although not in the same rank as the other categories listed, is an important taxon in the history of the creediid fishes; its taxonomic limits closely resembles what is presently known as family Creediidae.

Authorship was established for all suprageneric taxa listed below, except for the Trichonotidae. The reference given after the Trichonotidae represents only the first inclusion of a creediid species in that family (for a more detailed account on the taxonomic history of creediids, see "Historical review"). A summary of the main classificatory schemes proposed to creediids can be found in Table 1.

Family Creediidae

Type Genus Creedia (Ramsay, 1881)

Trichonotidae (in part).Waite, 1881 (Hemerocoetes haswelli).

Creediadae. Waite, 1899 : 63 (type-species Creedia clathrisquamis).

Emended to Creediidae by Waite, 1899.

Creediidae. Waite, 1899, emendation from Creediadae, in erratum slip.

Limnichthyidae. Regan, 1913: 142.

Limnichthyinae. Schultz, 1943: 261.

IV.2. FAMILY DIAGNOSIS AND DESCRIPTION

The following diagnosis includes both external morphology and osteological features. Characters thought to be synapomorphic for the Creediidae are identified as such in the phylogenetic analysis. The description mostly includes external morphological characters. A more detailed account of the osteological characters is given in the section on comparative osteology. A more detailed account of the geographic distribution and coloration is given in the section on species description.

DIAGNOSIS: upper jaw with translucent fleshy extension extending beyond lower jaw; lower jaw bordered by cirri; eye protruding; lateral line descending at pectoral fin tip and posteriorly running near the ventral profile of body; most lateral line scales with a central expanded lobe; dorsal and anal fins spineless; opercular bones splintered; cleithrum with a posteriorly directed spine beneath its posterior tip; pelvis cup-shaped, with a medially directed pelvic spur; ectopterygoid with a fan-shaped posterior tip attached to the quadrate and metapterygoid; lower arm of posttemporal much reduced, not reaching ventral surface of skull; gill rakers only present on lower limb of arch.

DESCRIPTION: Small (up to 86 mm total length) trachinoid fishes, with an elongate, anteriorly sub-cylindrical and posteriorly compressed body (body deeper and more compressed in Schizochirus); head moderately depressed, tapered anteriorly; eyes near the dorsal profile of head, protruding; mouth cleft nearly horizontal, jaws equal; upper jaw with translucent fleshy extension, projected beyond lower jaw; margin of upper jaw

with minute cirri in Creedia spp. (character could not be checked in C. bilineatus) and Tewara ; tip of maxilla extending to a vertical at the centre of eye (most Creedia spp.) or reaching or extending beyond posterior margin of eye; lower jaw with a dorsal knob at symphysis and bordered by cirri; two pairs of nostrils, the anterior one small, pore-like in Creedia, large with nasal rosette filaments exposed in Schizochirus, and enclosed in a tube in the other genera; posterior nostril pore-like in all genera (a small flap is present on its anterior margin in Schizochirus); lower margin of orbit with skin fold in Creedia spp. Interorbital space narrow, with one or two pores posterodorsally; four infraorbitals, the lacrymal the largest, with a transversal groove in Schizochirus and a posteroventral projection in all genera but Schizochirus, the second one much reduced (except in Schizochirus and Creedia), the third with a ventral flange (except in Schizochirus); fourth infraorbital a very small tube firmly attached to the sphenotic (largest in Schizochirus); cheeks scaled in Schizochirus, Limnichthys (one or two scales in L. nitidus) and Tewara, with a pocket of small embedded scales in Creedia, and scaleless in the other genera. Body entirely or partially covered by cycloid scales (only lateral line scales present in Crystallodytes), lateral line with 34-60 scales, descending at pectoral fin tip and running parallel to the ventral profile of body, its scales (except for the first 10-15) with a central expanded lobe, markedly trilobed in Limnichthys and Tewara. Base of caudal fin partially covered by one to three scales. Dorsal fin single, without spines, with 12-41 biserial, segmented rays; pectoral fin with 11-16 unbranched rays (except for Schizochirus and Creedia partimsquamigera, in which the rays are branched); pelvis cup-shaped, pelvic fin with one spine and three to five unbranched (except for Schizochirus) rays, or absent (Apodocreedia), its origin in advance of pectoral fin base; each basipterygium with a medially directed pelvic spur on its posterolateral margin. Anal fin single, without spines, with 22-40 unbranched rays (except for Schizochirus); caudal fin truncate, with 8 or 9 branched rays; 1 or 2 epurals; hypurapophysis absent. Vertebrae 37-59, one set of

epipleural ribs, starting from first vertebra; pleural ribs absent (for a more complete osteological description, see section on osteology). Gill membranes not united, free from isthmus, ventral opercular membranes overlapping each other; seven branchiostegal rays, slightly increasing in size from first to seventh. About six to 13 short gill rakers on the lower limb of the branchial arch. No gill rakers on the upper limb.

DISTRIBUTION: Creediids occur in tropical and subtropical areas of the Indo-Pacific (between latitudes 40°N and 55°S), from the Red Sea and South Africa to the Sea of Japan, New Zealand, Hawaii and Easter Island.

COLORATION IN ALCOHOL: Most creediids possess between six to 18 brown saddle marks along the upper half of body, usually connected ventrally to a horizontal stripe, and brown speckles on head and fins.

The color pattern of live specimens of some creediid species has been described. The body and the fins are described as translucent, the markings on body generally having a conspicuous color.

DEPTH: Based on collection records, most creediid species occur in shallow waters, between zero and 45 m, except for Limnichthys rendahli, which occurs in deeper waters; specimens belonging to lot NMNZ P3287 were collected at 165 m.

KEY FOR THE GENERA OF CREEDIIDAE

1a. Dorsal fin with 19-41 rays.....2

1b. Dorsal fin with 11-16 rays.....Creedia Ogilby

2a. Head of premaxilla toothless; anal fin rays unbranched.....3

2b. Head of premaxilla toothed; anal fin rays branched.....Schizochirus Waite

3a. Pelvic fin present, with four or five rays.....4

3b. Pelvic fin absent.....Apodocreedia de Beaufort

4a. Scales on body not confined to lateral line.....5

4b. Scales on body confined to lateral line.....Crystallodytes Fowler

5a. Lateral line scales trilobed; cirri on lower hyoid arch present.....6

5b. Lateral line scales elongate, with central expanded lobe; cirri on lower hyoid arch absent..... Chalixodytes Schultz

6a. Anal fin rays 22-34.....Limnichthys Waite

6b. Anal fin rays 36-39.....Tewara Griffin

V. SPECIES DESCRIPTION

The following section includes comparative descriptions of all valid species of Creediidae which are based solely on the examined material. Minimum and maximum values of the standard length (SL) for the examined specimens of all species are given in parentheses, at the beginning of the descriptions.

Schizochirus Waite, 1904

Schizochirus Waite, 1904, Rec. Aust. Mus. 5(4) : 241 (type-species Schizochirus insolens, by monotypy).

DIAGNOSIS: Posterior nostril with a distinct flap on anterior margin; pectoral fin rays with 16-17 rays, lower ones (from about 7th to 14th ray) longer and thicker than upper ones; first four anal pterygiophores laterally expanded and converging to 1st haemal spine; nasal bone with lateral flange; four squarish infraorbitals, anal fin rays branched; two postcleithra; head of vomer with a block of conical teeth on each side; head of premaxilla with a patch of canine-like teeth.

One species, Schizochirus insolens. Fig. 1A.

DISTRIBUTION: Eastern Australia - Queensland and New South Wales. Fig. 2.

Schizochirus insolens Waite, 1904

Schizochirus insolens Waite, 1904, Rec. Aust. Mus. 5(4) : 242, plate 26, figs. 33-34. Type locality: Maroubra Bay, New South Wales, Australia. Syntypes: AMS I. 6758-9 (2 specimens).

CITATIONS: Marshall, 1928 : 193; McCulloch, 1929 : 334; Schultz, 1943 : 261; Schultz in Schultz et al., 1960 : 274; Nelson, 1978 : 408; Springer, 1982 : 38; Nelson, 1984 : 341; Nelson, 1985 : 283, 285-292; Nelson, 1986 : 4, 5.

MATERIAL EXAMINED: CSIRO B1165 (1), Kirra, Queensland, ca. 28°10'S, 153°32'E; AMS IA. 7062 (1), Balina, New South Wales, ca. 28°50'S, 153°31'E; AMS IB. 514 (2, 1 C+S), Mooloolabah, Queensland, ca. 26°46'S, 153°07'E.
Total number of specimens: 4.

DIAGNOSIS: Same as diagnosis of genus.

DESCRIPTION (23.5 - 51.7 mm SL): morphometrics and meristics are respectively given in Tables 7 and 3-6. Head convex in dorsal profile, with a gradual slope from the posterior margin of eye to tip of snout; body deeper than in the other creediids. Upper jaw fleshy extension poorly developed, projecting very little beyond lower jaw; maxilla extending sligthly beyond posterior margin of eye, posterior tip deeply notched; upper lobe of notch of maxilla smallest, not concealed under sheath when mouth closed. Lower jaw with conspicuous knob at symphysis and bordered by fleshy cirri. Anterior nostril a

large pore, nasal rosette filaments readily seen through it; posterior nostril with a flap on its anterior margin. Eyes dorsolateral, with slit-like extension in two specimens. Cheeks mostly covered by large cycloid scales; tongue free, longer than wider, with laterally expanded blunt tip; ventral opercular flaps not overlapping each other, posterior margin of opercular membranes covering base of pectoral fin rays; intercalar, interopercle and subopercle splintered, preopercular margin with some faint indentations (on the C+S specimen), margin of opercle entire; membrane joining the posterior margins of subopercle and opercle with cirri-like projections along its free margin; epihyal and ceratohyal with cirri along their orsal margin. Body completely scaled, except for pectoral fin base and isthmus; interpelvic space covered by a large scale; two scales covering base of caudal fin rays. Head of each premaxilla with two canine-like teeth and ca. 3-5 smaller ones; upper and lower jaws with a row of conical teeth, plus some sparsely distributed ones which do not form a complete row. Head of vomer with a block of conical teeth on each side; palatine with few teeth, clearly seen in two specimens. Anal and pectoral fin rays branched, dorsal fin rays unbranched. Anal fin origin preceding origin of dorsal fin by 4 to 5 rays, its end immediately before caudal peduncle. Dorsal fin ending 4 to 5 rays before the end of the anal fin. Pelvic fin tip separated from the anus by approximately seven scales. Lateral line gradually descending to ventral side of body at pectoral fin tip, then running parallel to and ca. two scale rows from anal fin base; lateral line scales markedly incised, with an expanded, blunt central lobe, extending very little beyond scale margin (first 13-14th scales with entire margin or very weakly incised and without lobe); tip of lateral lobes pointed.

COLORATION IN ALCOHOL: Uniform light brown, with vestiges of dorsal saddle marks in one specimen. Iris golden in one specimen, black in the other non C+S material.

DISTRIBUTION: same as distribution of genus.

REMARKS: S. insolens is represented in collections by few specimens; nothing has been reported on its way of life, except for Waite's (1904b) mention of numerous amphipods, copepods and isopods in the gullet and stomach of two specimens. Nelson (1985), based on limited comparative osteological data, indicated that, among creediids, Schizochirus most closely resembled the percophid condition (with regard to four characters); he considered it to be the most primitive (as well as the most distinctive) creediid genus.

Creedia Ogilby, 1898

Creedia Ogilby, 1898, Proc. Linn. Soc. N. S. W. , 23 (3) : 298 (type-species Creedia clathrisquamis, by original indication).

DIAGNOSIS: 12-16 dorsal fin rays; nostrils small, pore-like; lateral line scales posterior to the pectoral fin tip with expanded central lobe and pointed lateral lobes.

DISTRIBUTION: Australia (including Tasmania), Japan. Fig. 2.

Four species: Creedia haswelli, C. alleni, C. partimsquamigera and C. bilineatus. Fig.1B.

CITATIONS: Schultz in Schultz et al., 1960 : 274; Springer, 1982 : 38; Nelson, 1984 : 341; Nelson, 1985 : 292; Nelson, 1986 : 5; Shimada & Yoshino, 1987 : 123, 125, 126.

DIAGNOSIS: Dorsal fin with 12-16 rays; nostrils small, pore-like; ascending process of premaxillae anteriorly widely separated from one another; lateral line abruptly descending at pectoral fin tip, and then running parallel to ventral profile; angular dorsally with well developed flange, almost reaching the ectopterygoid.

KEY FOR CREEDIA SPECIES

1a. Body fully scaled; snout gradually sloping in dorsal profile.....2

1b. Body partially scaled; snout markedly convex.....C. partimsquamigera Nelson

2a. Pelvic fin formula I, 3.....3

2b. Pelvic fin formula I,4.....C. haswelli (Ramsay)

3a. Anal fin origin opposite dorsal fin origin.....C. bilineatus Shimada & Yoshino

3b. Anal fin origin much in advance of dorsal fin origin..... C. alleni Nelson

Creedia haswelli (Ramsay, 1881)

Hemerocoetes haswelli Ramsay, 1881, Proc. Linn. Soc. N. S. W. , 6 (3) : 575.

Type locality: North Head, Port Jackson, Australia.

Creedia clathrisquamis Ogilby, 1898 , Proc. Linn. Soc. N. S. W. , 23 (3) : 299.

Type locality: Maroubra Beach, near Sydney. Holotype: AMS I. 4259.

Creedia haswelli (Ramsay, 1881). Waite, 1904 : 57.

CITATIONS: Waite, 1899 : 63 (as Creedia clathrisquamis); Regan, 1913: 142 (as C. clathrisquamis); McCulloch, 1929 : 333; Scott, 1969 : 170; Scott, 1982 : 19-30; Nelson, 1978: 361; Nelson, 1985 : 408; Nelson and Randall, 1985 : 283, 285, 287, 288, 290, 291.

MATERIAL EXAMINED: AMS I. 23413-001 (1), off Low Point, Great Australian Bight, ca. 35°27'S, 139°20'E; AMS IA. 7118-7119 (2), off Jarvis Bay, A. C .T.; AMS I. 23415-001 (1), off Shoal Cape, Great Australian Bight, ca. 33°51'S, 121°10'E; AMS I. 9002 (1, C+S), Westernport, Victoria; AMS I. 23414-001 (1), off Eastern Group, Great Australian Bight, ca. 28°43'S, 113°48'E; AMS I. 23412-001 (2), off Head of Great Australian Bight, ca. 31°30S, 131°10'E; AMS I. 10412 (2, 1 C+S), South of Francis Island, S. A., ca. 16°53'S, 139°03'E; AMS I. 26397-002 (2), off Broken Bay, New South Wales, 33°51'S, 151°18'E; NMV A5819 (9), Western Bass Strait, 25 km S of Cape Otway, Victoria; NMV A2221 (7), Bass Strait, SW of Cape Otway; NMV 2219 (25), Bass Strait, 39°06'S, 143°35.8'E; NMV A3459 (69, three C+S), N.W. Tasmania, off Three Hummock, 40°23'S, 145°03'E; NMV A2223 (58, 2 C+S), Bass Strait, 39°01'S, 143°22.1'E; NMV A7767 (2), Eastern Bass Strait, 19 Km E of LakeTyers Entrance, Victoria; NMV A2222 (1) Bass Strait, SW of Cape Otway, 39°06'S, 143°07.4'E; NMV A2225 (11), Bass Strait, 39°02'S, 143°15.1'E; NMV A3849 (6), Silver Gull, Victoria, 37°50'S, 148°40'E. Total number of specimens: 198.

DIAGNOSIS: Pelvic fin formula I,4; pectoral fin rays 11-13; anal fin origin much in advance of dorsal fin origin; third infraorbital with anteriorly directed process.

DESCRIPTION (24.9 - 39.7 mm SL): morphometrics and meristics are respectively given in Tables 8 and 3-6. Snout relatively elongate, gradually sloping in dorsal profile; upper jaw fleshy extension projecting well beyond lower jaw, tapering towards tip. Maxilla extending to a vertical at center of eye, tip notched; upper lobe of notch smallest, concealed under sheath when mouth closed. Lower jaw with knob at symphysis, bordered by fleshy cirri; some minute cirri on upper jaw; nostrils pore-like; anterior nostril approximately on midline of snout, posterior one very close to it; eyes dorsal, with a skin fold along lower margin. Cheeks with a pocket of small, partially embedded cycloid scales; tongue free, longer than wider, slightly laterally expanded at blunt tip. Lateral line scales incised, with central expanded lobe (first 11-13 scales not incised and without lobe); central lobe of scales with cirri-like extension in most specimens (regardless of sex). Lateral line abruptly descending at pectoral fin tip, and then running parallel to anal fin base. Body completely scaled, except for pectoral fin base and isthmus; fins naked. Head of each premaxilla with two elongate, canine-like teeth and a few smaller ones. Upper and lower jaws with one row of conical teeth; posterior portion of dentary with a cluster of enlarged teeth; vomer with few conical teeth, few palatine teeth in some specimens. Ventral opercular membranes overlapping each other, opercular flap reaching origin of pectoral fin rays; margin of preopercle, interopercle and subopercle splintered, margin of opercle entire. Epihyal and ceratohyal with cirri along dorsal margin. Dorsal and anal fin rays unbranched; anal fin origin much in advance of dorsal fin origin, its end separated from the caudal peduncle by ca. two scales distance; dorsal fin end ca. 4 to 5 rays before end of anal fin. Pectoral fin rays unbranched, longer in males, pelvic fin rays longer in males, tip of pelvic fin separated from anus by ca. 8-9 scales.

COLORATION IN ALCOHOL: Background light brown, with black speckles on occiput. Margin of scales with vestige of black pigmentation in one specimen (also noted by Waite, 1899).

DISTRIBUTION: Southeastern Australia (including Tasmania); Southwestern Australia. See Fig. 2.

REMARKS: In external morphology and meristic counts, C. haswelli is more similar to C. alleni than to the other Creedia species. The two species are the only creediids to have cirri-like extensions on central lobe of lateral line scales. Creedia haswelli can be distinguished from C. alleni by the number of pelvic fin rays and the shape of the epurals (see diagnosis of C. alleni).

Creedia alleni Nelson, 1983

Creedia alleni Nelson, 1983, Proc. Biol. Soc. Wash. 96 (1) : 29, figs. 1A-B, 2A, 3. Type locality: off Garden Island, near Fremantle, Western Australia, 32°14.7'S,115°39'E. Holotype: WAM P25808-005; paratypes: WAM P25346-028, WAM P25347-001.

CITATIONS: Nelson, 1985 : 408; Shimada & Yoshino, 1987 : 123, 125, 126.

MATERIAL EXAMINED: WAM P25808-005 (1, holotype), off Garden Island, near Fremantle, Western Australia, 32°15.7'S, 115°39'E; WAM P25346-028 (1,paratype), off Gage Roads, Carnac Island, between Rottnest and Fremantle, Western Australia, 32°02'S, 115°40'E. Total number of specimens: 2.

DIAGNOSIS: Two tear-shaped epurals with apex at distal end (Nelson, 1983); pelvic fin formula I, 3; anal fin much in advance of dorsal fin origin.

DESCRIPTION (30.5 - 40.0 mm SL) **:** morphometrics and meristics are respectively given in Tables 9 and 3-6. Snout relatively elongate, gradually sloping in dorsal profile; fleshy extension projecting well beyond lower jaw, tapering towards tip. Maxilla extending to a vertical at center of eye, tip notched; upper lobe of notch smallest, concealed under sheath when mouth closed. Eyes dorsal, with skin fold along lower margin (less developed than the one found in C. haswelli); lower jaw with knob at symphysis, bordered by fleshy cirri; few minute cirri on upper jaw. Nostrils pore-like; cheeks with a pocket of partially embeded cycloid scales; tongue free, longer than wider, with slight lateral expansion at blunt tip. Lateral line abruptly descending at pectoral fin tip, then running parallel to anal fin base; lateral line scales incised,with central expanded lobe; some with cirri-like projections along central lobe margin; two scales covering base of caudal fin rays. Body completely scaled, except for pectoral fin base and isthmus. Head of each premaxilla with two canine-like teeth and a few smaller ones. Upper and lower jaws with one row of conical teeth ; no vomerine teeth were seen in the paratype (the vomer of the holotype seemed to bear two weakly developed teeth); palatine with few teeth (clearly seen on the holotype). Ventral opercular membranes overlapping each other, opercular flap reaching origin of pectoral fin

rays; interopercle and subopercle splintered, opercle entire; preopercle with some indentations (clearly seen only on holotype). Epihyal and ceratohyal with cirri along dorsal margin; dorsal and anal fin rays unbranched; anal fin origin much in advance of dorsal fin origin, its end separated from caudal peduncle by ca. two scales distance. Dorsal fin end approximately three rays before end of anal fin. Pectoral fin rays unbranched, pelvic fin tip separated from anus by ca. 12 scales.

COLORATION IN ALCOHOL: Uniform brown, with black speckles on occiput, along dorsal and anal fin bases, and on caudal fin. No color pattern observed by Nelson (1983).

DISTRIBUTION: Southwestern Australia. See Fig. 2.

REMARKS: Nelson (1983) pointed out the similarities between C. alleni and C. haswelli. He used the pelvic fin formula as the main character to separate this species from C. haswelli and remaining creediids; he also indicated that perhaps the shape of the epurals was also unique to C. alleni. Four years after Nelson's publication, Shimada & Yoshino (1987) described a new species of Creedia from Japan, which also had the pelvic formula of I,3. This rendered the separation between C. alleni and C. haswelli (based on external morphology characters) difficult. The tear shaped hypurals, however, are unique to C. alleni . The epurals of the other Creedia species are somewhat elongate and laterally expanded on the ventral side. Perhaps an edentulous vomer is also unique to

C. alleni, but that character needs to be checked in more specimens (after examining the two specimens I had access to in my study, I could not be conclusive about that character).

Creedia partimsquamigera Nelson, 1983

Creedia partimsquamigera Nelson, 1983, Proc. Biol. Soc. Wash. 96 (1) : 33, fig. 4.

Type locality: Cooge Beach, Sydney, N. S. W., 33°56'S, 151°16'E. Holotype: AMS I. 21420-001.

CITATIONS: Nelson, 1985 : 283, 285-87, 289-292; Nelson and Randall, 1985 : 408; Nelson, 1986 : 3, 5.

MATERIAL EXAMINED: AMS I. 21420-005 (2), Coogee Beach, Sydney, N. S.W., 33°56'S, 151°16'E. Total number of specimens: 2.

DIAGNOSIS: Snout convex in dorsal profile, shorter than in the other Creedia species; anterior half of body scaleless, except for two rows of partially embedded scales between the lowermost portion of pectoral fin and origin of pelvic fin; males with some pectoral fin rays branched (Nelson, 1983).

DESCRIPTION (59.1 - 66.3 mm SL): morphometrics and meristics are respectively given in Tables 10 and 3-6. Snout shorter than in the other Creedia species, convex in dorsal profile. Upper jaw fleshy extension slightly less developed than in the other Creedia species; maxilla extending to posterior margin of eye, tip weakly notched, concealed under sheath when mouth closed. Eyes smaller than in the remaining Creedia species, with skin fold covering lower margin; lower jaw with knob at symphysis, bordered by small, blunt cirri; few minute cirri on upper jaw. Nostrils pore-like; cheeks without scales; tongue free, longer than wider, with very slight lateral expansion at blunt tip. Lateral line abruptly descending at pectoral fin tip, lateral line scales incised, with central expanded lobe (first 11-12 without expanded lobe), lateral lobes pointed. Scales on body as follows: two rows between the lowermost portion of pectoral fin base and origin of pelvic fin; a row anteriorly extending to a midpoint between 1st dorsal ray and nape continuing onto dorsal fin base; caudad from approximately 5th dorsal fin ray level; a single scale on base of caudal fin rays; body otherwise naked. Head of each premaxilla with a patch of canine-like teeth; upper and lower jaws with one row of conical teeth; upper jaw teeth starting approximately at midpoint of bone length; lower jaw teeth enlarged at posterior portion of dentary. Vomer with few conical teeth, palatine edentulous. Ventral opercular membranes overlapping each other, opercular flap reaching base of pectoral fin. Dorsal and anal fin rays unbranched; anal fin origin much in advance of dorsal fin origin, its end ca. three scales distance from caudal peduncle. Dorsal fin ending ca. six rays before end of anal fin; pectoral fin rays unbranched; pelvic fin rays unbranched (however, see remarks). Interopercle and subopercle splintered, some indentations on preopercle; margin of opercle entire; few cirri on lower hyoid arch.

COLORATION IN ALCOHOL: Uniform cream, with black spackles on occiput. Nelson (1983) describes the coloration of C. partimsquamigera as follows: "little to no color pattern is apparent in the preserved material. However, in color transparencies provided by R. H. Kuiter of the 64 mm paratype there are two stripes extending along the length of the body, one dorso-lateral and the other mid- lateral, and about five short, closely set saddles just behind the nape".

DISTRIBUTION: Eastern Australia: New South Wales. See Fig. 2.

REMARKS: This species can be readily distinguished by the markedly convex snout and the only partially scaled body; the two rows of scales between the pectoral and pelvic fins is unique to C. partimsquamigera. It also presents marked sexual dimorphism in pectoral and pelvic fin lengths, as well as in the branched pectoral rays (Nelson, 1983).

Creedia bilineatus Shimada & Yoshino, 1987

Creedia bilineatus Shimada & Yoshino, 1987, Japan. J. Ichthyol., 34 (2) : 123, figs.1-5. Type locality: Yaeyama Islands, Ryukyu Islands, Japan. Holotype: URM-P (Department of Marine Sciences, University of Ryukyus) 6462, Kabira Bay, 24°09'N, 124°27.5'E, Ishigaki Island, Yaeyama Islands, Okinawa Pref., Japan.

MATERIAL EXAMINED: URM-P 6463 (1 C+S, partially dissected paratype), Kabira Bay, 24°09'N, 124°27.5'E, Ishigaki Island, Okinawa Pref., Japan. Total number of specimens: 1.

DIAGNOSIS: Anal fin with 17-18 rays (Shimada & Yoshino, 1987), its origin opposite origin of dorsal fin.

DESCRIPTION (32.0 mm SL)**:** limited morphometrics and meristics are respectively given in Tables 11 and 3-6 (for additional descriptive information see Shimada & yoshino, 1987). Maxilla extending to vertical at center of eye, tip weakly notched; lower jaw with knob at symphysis, bordered by small cirri; eyes dorsal, with a fold of skin covering lower margin. Head of each premaxilla with a patch of canine-like teeth; upper and lower jaws with one row of conical teeth; head of vomer with a pair of canine-like teeth on each side, palatine edentulous; opercular flap reaching base of pectoral fin; interopercle weakly indented, subopercle splintered; no indentations on preopercle and opercle. Dorsal and anal fin rays unbranched; anal fin origin opposite origin of dorsal fin, its end ca. three scales distance from caudal peduncle; pectoral and pelvic fin rays unbranched; pelvic fin tip separated from anus by ca. 12 scales distance (judging from scale impressions).

COLORATION IN ALCOHOL: Since the only available specimen was cleared and stained, no coloration could be observed. A color plate and a short description of both the fresh coloration and the coloration of preserved specimens of C. bilineatus are provided

by Shimada & Yoshino (1987): Fresh specimens have a whitish body with two yellowish brown stripes, one dorso-lateral, the other mid-lateral; the fins are transparent. Preserved specimens have a pale body, and the two stripes are not apparent.

DISTRIBUTION: Only known from the Yaeyama Islands, Japan. See Fig. 2.

REMARKS: This is the only non-Australian species of Creedia. Shimada and Yoshino (1987) remarked that C. bilineatus was closely related to C. alleni in the number of pelvic fin rays, but was distinguished from it (and from other Creedia species) by a combination of meristic counts. However, Creedia bilineatus can also be separated from the remaining Creedia species by the presence of a pointed tongue (fide Shimada & Yoshino, 1987).

Tewara Griffin, 1933

Tewara Griffin, 1933, Transactions and Proceedings of the New Zealand Institute, 63, part 2, : 174 (Type-species: Tewara cranwelli Griffin,1933, by monotypy. Emended to T. cranwellae).

DIAGNOSIS: Dorsal fin rays 36 - 40; anal fin rays 36-39; upper jaw fleshy extension less developed than all other creediids but Schizochirus; dorsal saddle marks short, ventrally connected by a narrow band.

DISTRIBUTION: New Zealand: North and South Islands down to Foveaux Strait. Fig. 2.

One species, Tewara cranwellae. Fig. 1C.

Tewara cranwellae Griffin, 1933

Tewara cranwelli Griffin, 1933, Transactions and Proceedings of the New Zealand Institute, part 2 : 174, plate 25. Type locality: Smugglers' Bay, New Zealand. Holotype: AIM (Auckland Institute and Museum).

Tewara cranwellae (emendation). Whitley, in Graham, 1956 : 410.

CITATIONS: Schultz, 1943 : 261; Schultz in Schultz et al., 1960 : 275; Nelson, 1978 : 352-356, 360, 361; Nelson, 1979 : 273, 274, 276; Springer, 1982 : 38; Nelson, 1983 : 34; Nelson, 1984a : 341; Nelson, 1985 : 283, 284, 287, 289-290, 292; Nelson and Randall, 1985 : 404, 408.

MATERIAL EXAMINED: NMNZ P 1758 (2), inside Otago Heads, New Zealand; NMNZ P 6246 (7, 2 C+S), Western Island Bay, Wellington, 41°21'S, 174°46'E; NMNZ P 7390 (1), South Bay, Kaikoura, 42°26'S, 173°41'E; NMNZ P18146 (8, 2 C+S), Mangati Reef, New Plymouth, 39°01'S, 174°09'E; NMNZ P 21223 (6), Goose Bay, Kaikoura, 42°29.4'S, 173°31.3'E; NMNZ P7390 (1), South Bay, Kaikoura,

42°26'S, 173°41'E; ANSP 122762 (69), New Zealand, North Island, Bay of Islands, N end of the smaller island just NW of Urupukapuka Island. Total number of specimens: 94.

DIAGNOSIS: same as diagnosis of genus.

DESCRIPTION (36.2 - 71.2 mm SL): morphometrics and meristics are respectively given in Tables 12 and 3-6. Snout gradually sloping in dorsal profile; upper jaw extension moderately developed; maxilla reaching or slightly beyond posterior margin of eye, posterior tip not notched (a very shallow notch in a few specimens); lower jaw with knob at symphysis and bordered by pointed cirri; few minute cirri on upper jaw. Anterior nostril enclosed in a tube, posterior one pore-like, situated adjacent to anterior margin of orbit; eyes dorsal; cheeks partially covered by cycloid scales; tongue free, longer than wider, with pointed tip. Lateral line scales trilobed (first 10-11th not trilobed), lobes with rounded margins, lateral line gradually descending at pectoral fin tip, then running parallel to anal fin base (ca. two scale rows above anal fin base for ca. 3/4 of body length, then one row above anal fin base). Body completely scaled, except for pectoral fin base and isthmus. No teeth on head of premaxilla, ca. two to four rows of conical teeth on jaws (dentary sometimes with a single row of smaller teeth almost reaching symphysis); small teeth on vomerine head, palatine edentulous. Ventral opercular flaps overlapping each other, posterior margin of opercle reaching base of pectoral fin rays. Interopercle, subopercle and articular splintered, margin of preopercle and opercle entire; cirri on dorsal margin of epihyal and ceratohyal. Anal fin origin one to two rays in advance of dorsal fin origin, its end ca. two scales distance from caudal peduncle; dorsal fin end opposite anal fin; dorsal, anal and pectoral fin rays unbranched, pelvic fin tip separated from anus by ca. seven to nine scales.

COLORATION IN ALCOHOL: Background light brown to cream; two brown bands, one running along midline of body, from upper margin of preopercle to caudal peduncle, the other parallel to and ca. two scale rows above the midline one. 12-18 dorsal saddles marks (first one on nape, last one ca. 2-3 scales distance from caudal peduncle), ventrally connected to the upper band; a fine brown vertical line on caudal peduncle.
Dorsal fin rays, base of anal fin, snout and lower jaw with vestige of dark brown color; dorsal side of head, most notably on occiput, with dark brown speckles (some specimens with denser, black pigmentation on head region).

DISTRIBUTION: same as distribution of genus.

REMARKS: Tewara was described from a single specimen, to include T. cranwelli. Later, Whitley (in Graham, 1956; not 1965, as shown in Nelson, 1978) emended cranwelli to cranwellae, which has been the spelling adopted since then. Tewara externally resembles Limnichthys, but the two genera can be separated on the basis of their color pattern and number of dorsal and anal fin rays.

Limnichthys Waite, 1904

Limnichthys Waite, 1904, Rec. Aust. Mus., 5 (3) : 178 (Type- species Limnichthys fasciatus, by monotypy).

DIAGNOSIS: Dorsal fin rays 21-33; anal fin rays 23-34; lateral line scales distinctly trilobed, the central lobe much larger than the lateral ones.

CITATIONS: Regan, 1913: 143; McCulloch, 1929 : 334; Smith, 1958 : 248; Schultz, 1943 : 261; Smith, 1961 : 736, 737; Schultz in Schultz et al., 1960 : 278; Nelson, 1978 : 352, 355, 356, 359, 360, 361; Springer, 1982 : 39, 158; Nelson, 1984 :341; Nelson, 1985 : 285, 289, 291, 292.

DISTRIBUTION: This genus is widely distributed in the Indo-Pacific. Fig. 3.

Four species: Limnichthys fasciatus, L. nitidus, L. rendahli and L. polyactis. Fig. 1D.

KEY FOR LIMNICHTHYS SPECIES

1a. Dorsal fin rays 20-28.....2

1b. Dorsal fin rays 29-33.....3

2a. Origin of dorsal fin anterior to origin to anal fin.....L. polyactis Nelson

2b. Origin of dorsal fin on same vertical or posterior to anal fin origin...L. rendahli Parrott

3a. Five to eight dorsal saddle marks, mostly connected to midlateral band; anal fin rays 24-29.....L. fasciatus Waite

3b. 7-13 short dorsal marks, usually none connected to the weakly developed midlateral band (band may be absent); anal fin rays 22-27.....L. nitidus Smith

Limnichthys fasciatus Waite, 1904

Limnichthys fasciatus Waite, 1904, Records of the Australian Museum, 5 (3) :178, plate XXIII, fig. 4. Type locality: Lord Howe Island, Australia.

Limnichthys fasciatus major. Whitley, 1945, 11(1):3.

CITATIONS: Waite, 1904b: 243; Waite, 1904c: 222; Waite, 1916a: 82; Whitley, 1945: 31; Aoyagi, 1952: 233; Matsubara, 1952: 90; Parrott, 1958: 116-118; Smith, 1958: 247, 249; Smith, 1958: 249; Kamohara and Yamakawa, 1968: 16; Nelson, 1978: 351-356, 358-360; Nelson, 1979: 276, 277; Randall, 1982: 197, 204; Nelson, 1983: 29, 34-46; Nelson, 1985: 283, 287, 288, 291; Nelson and Randall, 1985: 409; Okiyama (ed.), 1988: 730, 731.

MATERIAL EXAMINED: AMS I.27134-010 (36, 2 C+S), Middleton Reef, outer edge of lagoon, off NSW; AMS I.27141-009 (5), Middleton Reef, reef flat near wreck of "Fuku Maru"; ANSP 122824 (1), Australia, Queensland, Endeavour Reef, middle of N side of E half of reef, 15°45'S, 145°42'E; ANSP 122767 (1), Australia, Long Bay, near Sydney; ASZF 055859 (1), Southern Taiwan; BPBM 10802 (2), Heron Island; BPBM 14342 (4), One Tree Island; BPBM 17939 (18), Lord Howe Island; LACM 30823-10 (4), Australia, Sydney Harbour; LACM 36015-17 (2), Lord Howe Island; NMNZ P6245 (23, 3 C+S), McCauley Island, Kermadecs, 30°10'S, 179°30'W; NMV A3601 (6), Horseshoe Bay, Bermagui, New South Wales, 36°25'S, 150°04'E; NMV A5794 (3), Montague Island, Harbour, New South Wales; NMV A2137 (3), Bermagui, New South Wales; NMV A9509 (4), Manly, New South Wales; ROM 44170 (2), Fiji, Viti Levu,

18°82'02"S, 178°23'08"; ROM 44171 (3), Fiji, Viti Levu, 18°83'09"S, 178°23'21"E; ROM 44172 (1), Fiji, Great Astrolabe Reef, 18°45.5'02"S, 178°31'13"; ROM 44173 (18, 2 C+S), Fiji, Great Astrolabe Reef, 18°45.1'15"S, 178°31'59"E; ROM 42589 (1), Solomon Island, 09°28'90"S, 159°49'90"E; WAM 22569.00 (1), Kendrew Island, 22°29'S, 116°32'E; WAM 25758.020 (2), Rottnest Island, 32°01'S, 115°27'E; WAM WAM 26614.018 (2), Rottnest Island, 32°00'S, 115°28'E; WAM 28300.02 (19), Lucky Bay, 34°05'S, 122°15'E; WAM 28519.023 (19), Lucky Bay, 34°05'S, 122°15'E; WAM 28519.023 (6), Cape Naturalist, 33°32'S, 115°01'E; WAM 28520.022 (1), Canal Rocks, 33°39'S, 115°01'E; WAM 28538.018 (1), Coral Sea, Holmes Reef, 16°31'S, 147°50'E; WAM 121.001 (1), Garden Island, 32°12'S, 115°40'E; UAMZ uncatalogued (2, 1 C+S), Awakominato, Chiba, Japan; USNM 295851 (2 of 18, 1 C+S), Batanes, Philippine Is. Total number of specimens: 181.

DIAGNOSIS: Pelvic spur long, meeting along midline and extending posteriorly (all but one specimen, USNM 295851, examined for that character had the the pelvic spur as described above); five to eight dorsal saddle marks, mostly connected to a midline stripe; dorsal surface of articular bone with a pointed anteriorly directed projection.

DESCRIPTION (15.6-46.0 mm SL): morphometrics and meristics are respectively given in Tables 13 and 3-6 . Head moderately convex in dorsal profile, with a gradual slope from the posterior margin of eye to tip of snout. Upper jaw extension well developed, projecting beyond lower jaw; maxilla extending to or slightly beyond posterior margin of eye, posterior tip pointed, without notch; maxilla concealed under sheath when mouth closed. Lower jaw with knob at symphysis and bordered by cirri, mostly of uniform

length and without split tip. Anterior nostril enclosed in a tube, posterior one pore- like. Eyes dorsolateral, cheeks partially covered by cycloid scales or naked. Tongue free, longer than wider, with pointed tip. Lateral line scales trilobed (first 12-15 not trilobed); lateral line gradually descending at pectoral fin tip, than running parallel to anal fin base (ca. 2-3 scale rows above anal fin base for 3-4/5 of body length, then one scale row above anal fin base. Ventral opercular flaps overlapping each other, posterior margin of opercle covering base of pectoral fin. Interopercle and subopercle splintered, articular with some splintering, margin of opercle entire (one specimen showed some splintering on the opercle margin) . Epihyal and ceratohyal with cirri along their dorsal margin. Body completely scaled, except for pectoral fin base and isthmus. Two scales covering base of caudal fin rays. No teeth on head of premaxilla, maxilla with one row of conical teeth; dentary with one or two rows of conical teeth, starting about halfway between the symphysis and the labial comissure. Vomer with variable number of conical teeth; some specimens possess about two vomerine teeth, others between eigth and fifteen; no teeth on palatine. Pectoral and pelvic fin rays unbranched; anal fin origin ca. two to four rays behind the origin of dorsal fin, its end ca. one scale distance from caudal peduncle. End of dorsal fin opposite anal fin; tip of pelvic fin separated from anus by ca. six to eight scales.

COLORATION IN ALCOHOL: Background light brown, with five to eight brown to blackish dorsal saddle marks, most of them connecting via the ventral margin to a mid-lateral bar of the same color as the marks. There is much variation to this pattern; in some specimens the mid-lateral stripe is wider, darker (mostly in the New Zealand and Japan specimens). In others, the dorsal saddle marks are faint and narrow, but whenever coloration was still available at least two of the dorsal marks contacted the mid-lateral stripe. See Fig. 5.

DISTRIBUTION: Australia, New Zealand, Philippines, Japan, and few localities in the Central Pacific Ocean.

REMARKS: L. fasciatus major was decribed based on material from Western Australia. Whitley (1945) used larger body size and dorsal and anal fin counts to erect that subspecies. Nelson (1978) provisionally recognized L. fasciatus major and later (Nelson, 1983) indicated that "although there is no firm basis at present for recognizing a separate subspecies in Western Australia, further study is warranted of suspected differences between Western Australian material and that from elsewhere in the number of rows of teeth in the lower jaw and in the presence or absence of branching of the cirri bordering the lower jaw."

My examination of material previously identified as L. fasciatus major, as well as the P.C.A. analysis do not support recognition of the aforementioned subspecies. The number of tooth rows varies throughout the range of L. fasciatus. The lower jaw cirri were unbranched in most examined specimens, including the ones from Western Australia. The Western Australian specimens did not form a cluster of their own in the P.C.A. Rather, they fell within the range of the other specimens of L. fasciatus. L. fasciatus major is treated as a synonym of L. fasciatus.

Nelson and Randall (1985) pointed out differences regarding Fijian specimens with the colour pattern like L. fasciatus, but with lower meristic counts. In the P.C.A., I chose a distinct symbol for those specimens, to see how they would group. Figs. 6-9 show that the Fijian specimens fall within the range of the other specimens of L. fasciatus and should not be recognized as a separate taxon.

Limnichthys nitidus Smith

Limnichthys nitidus Smith, 1958, Annals and Magazine of Natural History, 13 (i) :247, fig. 1. Type locality: Pinda, Mozambique.

Limnichthys donaldsoni Schultz, 1960, USNM. Bulletin, 202 (2) :278, fig. 107. Type locality: Bikini Atoll, lagoon reef halfway betweeen Bikini and Amen Islands. Holotype: USNM 140906.

CITATIONS: Smith, 1961: 566; Nelson, 1978: 352,353,360,362; Nelson, 1979: 276; Nelson, 1985: 287, 288, 291; Nelson and Randall, 1985: 409; Nelson (1986), In Smith and Heemstra (ed.) : 737.

MATERIAL EXAMINED: ANSP 134987 (1), Seychelles Is., Faon Is. off S shore, 04°38'S, 55°30'E; ANSP 130679 (1), Cocos-Keeling Is., West Is., N end, 12°08'S, 96°49'15"E; ANSP 134990 (2), Seychelles Is., Mahe, Beau Vallon Bay, 04°37'S, 55°26'E; ANSP 134991 (1), Seychelles Is., Praslin vicinity, just S of Round Is., 04°37'S, 55°30'E; ANSP 130659 (1), Cocos-Keeling Is., West Is., off N end outside barrier reef, 12°07'S, 96°45'E; ANSP 134989 (2), Seychelles Is., Amirante Is., Vic. St, Joseph Is., SW of Ressource Is., 05°26'S, 53°22'E; ANSP 136599 (2), Seychelles; ANSP 134985 (2), Seychelles Is., Mahe Is., off N tip of island, 04°33'S, 55°26'E; ANSP 151601 (3), Seychelles Is., Mahe, Beau Vallon Bay, NW end, 04°37'S, 55°25"E; ANSP 134988 (1), Seychelles Is., Mahe Is., immediately S of North Point on W side of island, 04°43'S, 55°26'E; ANSP 151599 (1), Seychelles Is., Beacon Is., off S shore of island, 04°37'S,

53°31'E; ANSP 151600 (1), Seychelles Is., Amirante Is., D'arros Is., off E side of island, 05°25'S, 53°18'E; ANSP 134986 (1), Seychelles Is., Amirante IS., African Is., SE of South Is., 04°54'S, 53°23'E; ANSP 130658 (1), Cocos-Keeling Is., Direction Is., 12°05'S, 96°53'E; BPBM 31057 (4), Gulf of Aqaba, Sinai Peninsula, Red Sea; BPBM 21776 (1), South Africa, Natal, Kosi Bay; RUSI 76-32 (3), Kwazulu-Jeser Point ; RUSI 20070 (9), Natal: 6 miles S of Sodwana Bay; RUSI 3734 (1), Mozambique: Pinda; RUSI 76-16 (25), Kwazulu, 2.5 km S of Boteler Point; RUSI 76-356 (20), Natal: Chaka's Rocks; RUSI 20074 (7), Natal: Kosi Point; RUSI 76-10 (5), Kwazulu, reef off Sodwana Bay; RUSI 76-21 (50), Kwazulu: reef 6.5 km N of Island Rock; UAZM 5517 (3, C+S), Kwazulu, reef 6.5 km N of Island Rock; ROM 56636 (1), Comores, Indian Ocean; BPBM 13952 (3), Cook Is.; BPBM 16798 (1), Hawaiian Is.; BPBM 27800 (7, 2 C+S), Marshall Is.; BPBM 16886 (2), Pitcairn Is.; BPBM 16958 (2), Pitcairn Is.; BPBM 13953 (3), Cook Is., BPBM 16798 (1), Hawaiian Is.; BPBM 17086 (1), Henderson Is.; BPBM 17944 (1), Marshall Is.; BPBM 31013 (3), Hawaiian Is.; BPBM 31246 (1, C+S). Total number of specimens: 170.

DIAGNOSIS: seven to thrirteen short, narrow marks on dorsal profile of body, not connected to the poorly developed (or absent) midline stripe; one epural; dorsal surface of articular bone without projection.

DESCRIPTION (15.4-35.5 mm SL): morphometrics and meristics are respectively given in Tables 14 and 3-6 . Snout gradually sloping in dorsal profile; upper jaw fleshy extension projecting well beyond lower jaw; maxilla extending to posterior margin of orbit, tip not notched. Lower jaw with knob at symphysis and bordered by pointed cirri; anterior

nostril enclosed in a tube, posterior one pore-like, adjacent to anterior margin of orbit; eyes dorsolateral; cheeks with one or two scales adjacent to the tip of maxilla; tongue free, longer than wider, with pointed tip. Lateral line scales trilobed (first 12-15 not trilobed), lateral line gradually descending at pectoral fin tip, then running parallel to anal fin base (ca. two scale rows above anal fin base for about 2/3 of body length; then one row above anal fin base). Body completely scaled, except for pectoral fin base and isthmus. No teeth on head of premaxilla , two rows of conical teeth on upper jaw; lower jaw with two rows of conical teeth, one extending to knob. Small teeth on vomer , palatine edentulous. Ventral opercular flaps overlapping each other, posterior margin of opercle reaching base of pectoral fin rays. Interopercle and subopercle splintered; articular moderately splintered; preopercle and opercle entire; cirri on dorsal margin of epihyal and ceratohyal. Anal fin origin two to four rays behind origin of dorsal fin, its end ca. one scale distance from caudal peduncle; end of dorsal fin opposite anal fin; dorsal, anal and pectoral fin rays unbranched; tip of pelvic fin separated from anus by ca. five to seven scales.

COLORATION IN ALCOHOL: Background light brown to pale, with seven to thirteen short dorsal saddle marks (usually narrower than the ones found in L. fasciatus), not connected to the mid-lateral stripe, which is less developed than the one found in L. fasciatus (in a few examined specimens a maximum of two dorsal marks contacted the mid-lateral stripe). Specimens from the Central Pacific area seem to lack the midlateral stripe (see below).

DISTRIBUTION: Indo-Pacific, as far East as the Pitcairn Is; Red Sea. See Fig. 3.

REMARKS: L. nitidus and L. donalsoni are very similar in their external morphology, as well as in the meristic counts. As discussed below, the results of the P.C.A. show that the two nominal species cannot be separated on the basis of those characters. In the present study, they are regarded as conspecific, the name L. nitidus having priority.

Two subspecies are recognized for L. nitidus: L. nitidus nitidus Smith and L. nitidus donaldsoni, Schultz, for the following reason: there seems to be a difference in the color pattern of the Central Pacific specimens (previously identified as L. donaldsoni), which was noted by Schultz (1960), Nelson and Randall (1985), as well as by my own examination of the specimens for which the color pattern was preserved. As stated before, in L. nitidus the dorsal marks are short (which is also the case for the Central Pacific specimens, previously identified as L. donaldsoni) and do not reach the weakly developed midlateral band; in the specimens from the Central Pacific, however, the midlateral band seems to be absent. Unfortunately, the coloration had faded away in specimens from intermediate localities (such as the Cocos-Keeling area), and I could not be conclusive about that character (and for this reason did not further separate the character color pattern to include it in the P.C.A.). At present, the Central Pacific specimens will be recognized as a separate subspecies from the Indian Ocean specimens. When additional material in which the color pattern has been preserved becomes available, this claim should be re-analyzed. The two subspecies are recognized because, despite the overall similarity between L. nitidus and "L. donaldsoni" (as revealed by the P.C.A.), after examining the material at hand, I could not be conclusive about the distribution of the character color pattern of and felt that further work is still necessary before a decision to completely merge the two taxa is made. As pointed out by Mayr and Ashlock (1991), "sensible use of the category subspecies is still a convenient device for classifying population samples in geographically variable species." Recognition of subspecies, however, is a problematic procedure in taxonomy, and they should only be used as a classificatory device.

P.C.A. RESULTS:

Two separate datasets were used in the P.C.A.: morphometric characters and meristic counts (including attributes). The meristic dataset was further separated in two subsets, one including coloration and number of epurals, and another including the pelvic spur shape.

The three nominal species compared simultaneously:

The morphometric characters are poor discriminators for L. fasciatus, L. nitidus and L. donaldsoni. When the three species are compared, color pattern contributes the most to separate them; number of epurals and of anal fin rays are also important discriminators for the three taxa. L. fasciatus can be separated from L. nitidus even when the character color is excluded. However, all the specimens of the two nominal species cannot be correctly assigned even when including the character color (defined as dorsal marks short, as opposed to long, reaching a midlateral as in L. fasciatus). Scatter plots of factor 1 of the meristics plus attributes dataset (PC1) and of the morphometrics dataset for the three species are shown in Fig. 7.

Pairwise comparisons:

Pairwise comparisons were performed for the three nominal species, using factor 1 of the meristics dataset (PC1) and factor 2 of the morphometrics dataset (PC2). The results show distinct separation between L. fasciatus and L. nitidus when color is included in the

analysis; two clusters are still identifiable when color is excluded from the analysis. Pairwise comparisons between L. fasciatus and L. donaldsoni show two completely distinguishable clusters when color is included, which become less defined without the information on coloration. L. donaldsoni and L. nitidus, however, could not be completely separated even when color was added to the analysis. The scatter plots for the pairwise comparison comparisons are given in Figs. 7-9.

Although the morphometrics did not show any marked difference between L. fasciatus and L. nitidus, the meristics dataset (especially, but not necessarily, when color was added to it) separated L. fasciatus from L. nitidus. My findings suggest that, in spite of their overall similarity, those two species can be regarded as valid. The P.C.A. results find support in two osteological characters, which were not included in the P.C.A. because they could only be observed in a limited number of cleared and stained specimens: the projection on the articular (described for L. fasciatus) and the shape of the urohyal. In L. fasciatus, the posterior portion of the urohyal is entire, whereas in L. nitidus it is forked. L. donaldsoni (like L. nitidus), lacks the projection on the articular.

L. fasciatus and L. nitidus are recognized as valid species, the latter including to subspecies: L. nitidus nitidus and L. nitidus donaldsoni.

Limnichthys nitidus nitidus Smith

DIAGNOSIS: 9 to 13 short marks on dorsal profile of body, not connected to a weakly developed midlateral stripe.

DISTRIBUTION: Indian Ocean, including the Red Sea, as East as the Cocos-keeling area.

Limnichthys nitidus donaldsoni Schultz

DIAGNOSIS: 7 to 11 short marks on dorsal profile of body; midlateral band absent.

DISTRIBUTION: Central Pacific.

Limnichthys rendahli Parrott, 1958

Limnichthys rendahli Parrott, 1958, Records of the Dominion Museum, 3 (2): 116.Type locality: Auckland Islands. Holotype: CM 301.

CITATIONS: Robertson, 1973 : 351-354; Nelson, 1978: 273-276; Nelson, 1979 : 351-360; Nelson, 1984 : 404, 409.

MATERIAL EXAMINED: NMNZ P 1154 (6, 2 C+S), Foveaux Strait, Puapuke Oyster Bed; NMNZ P 6249 (5), NW Chatham Rise, 42°59.4'S, 175°30.5'E; UAMZ 3760 (12), Foveaux Strait, N. Z. Total number of specimens: 23.

DIAGNOSIS: origin of anal fin behind origin of dorsal fin; 13-16 unbranched pectoral fin rays; two epurals; dorsal margin of articular bone with a forwardly directed short projection.

DESCRIPTION (50.4 - 65.5 mm SL): morphometrics and meristics are respectively given in Tables 15 and 3-6. Snout gradually sloping in dorsal profile; upper jaw fleshy extension projecting well beyond lower jaw; maxilla extending to posterior margin of orbit, tip not notched. Lower jaw with knob at symphysis and bordered by pointed cirri; anterior nostril enclosed in a tube, posterior one pore-like, adjacent to anterior margin of orbit; eyes dorsal; cheeks covered by cycloid scales; tongue free, longer than wider, with pointed tip. Lateral line scales trilobed (first 12-13 not trilobed), lateral line gradulally descending at pectoral fin tip, then running parallel to anal fin base (ca. two scale rows above anal fin base for about 2/3 of body length; then one row above anal fin base). Body completely scaled, except for pectoral fin base and isthmus. No teeth on head of premaxilla, two rows of conical teeth on upper jaw; lower jaw with two rows of conical teeth, one extending to knob. Small teeth on vomer palatine edentulous. Ventral opercular flaps overlapping each other, posterior margin of opercle reaching base of pectoral fin rays. Interopercle and subopercle splintered; preopercle, articular and opercle entire; membrane connecting subopercle and opercle with cirri-like projections; cirri on dorsal margin of epihyal and ceratohyal. Anal fin origin one or two rays behind origin of dorsal fin, its end ca. one scale distance from caudal peduncle; end of dorsal fin opposite anal fin; dorsal, anal and pectoral fin rays unbranched; tip of pelvic fin separated from anus by ca. six to eight scales.

COLORATION IN ALCOHOL: Background light brown, with 7-9 dorsal saddle marks. Nelson (1978) mentions a lateral band which connects most saddle marks ventrally; most of the coloration had faded in the examined specimens and the band was not visible on them.

DISTRIBUTION: This species is known from several localities in New Zealand, from the Three King Is. to the Foveaux Strait. It has also been found on the Chatham and Auckland Islands. See Fig. 3.

REMARKS: In terms of its external morphology, this species closely resembles L. polyactis. However, the two species can be separated on the basis of the position of the origin of the dorsal and anal fins; they can also be separated by the number of epurals (two in L. rendahli, one in L. polyactis), and by the size of the projection on the articular bone. L. rendahli occurs in deeper waters than the the other creediids. Based on collection records for the examined material, it can be found at depths of at least of 165 m. Nelson (1978) mentions a "questionable record of 322 m."

Limnichthys polyactis Nelson, 1978

Limnichthys polyactis Nelson, 1978 , N. Z. Journal of Zoology, vol. 5 :353, figs. 1a, 2b.

Type locality: West end Island Bay, Wellington 41°21'S,174°47'E.

Holotype: NMNZ 6243.

CITATIONS: Nelson, 1979 : 273-276; Nelson, 1983 : 31, 34; Nelson and Randall, 1985 : 404, 409.

MATERIAL EXAMINED: UAMZ 3758 (1, paratype), West end Island,Wellington, 41o21'S, 174o47'E; NMNZ P13215 (13), Henderson Bay, 36°46'S, 173°08'E; NMNZ P13216 (5), Matai Bay, 38°04'S, 176°36'E; NMNZ P 14957 (42), Cape Maria Von Dieman, Motupao Island, N side bay, leeward, 34°28.3'S, 172°38.2'E; NMNZ P117204 (5), Princess Bay, Wellington, 41°21'S, 174°47'E; NMNZ P19885 (2, 1 C+ S), cut on N end of Chalky Island, Fiordland, 46°03'S, 166°33.6'E; NMNZ P 14322 (2), Waikato Bay, 34°50'S, 173°25'E. Total number of specimens: 70.

DIAGNOSIS: Dorsal margin of articular bone with an elongate, pointed, forwardly directed process; one epural; origin of dorsal fin in front of anal fin origin; pectoral rays almost invariably 12-13 (one specimen had 14).

DESCRIPTION (19.9 - 69.9 mm SL): morphometrics and meristics are respectively given in tables 16 and 3-6. Snout gradually sloping in dorsal profile; upper jaw fleshy extension projecting well beyond lower jaw; maxilla extending beyond posterior margin of orbit, posterior tip not notched, concealed under skin fold (suborbital fold of Nelson, 1978). Lower jaw with knob and bordered by cirri; anterior nostril enclosed in a tube, posterior one pore-like, situated adjacent to anterior margin of orbit; eyes dorsal, cheeks partially covered by cycloid scales; tongue free, longer than wider, with pointed tip. Lateral line scales trilobed (first 11-12 not lobed), lobes with rounded margins; lateral line gradually descending at pectoral tip, then running parallel to anal fin base (ca. three scale rows above anal fin base for ca. 3/4 of body length, then two rows above anal fin). Body completely scaled, except for pectoral fin base and isthmus. No teeth on head of premaxilla; one to two rows of conical teeth on upper jaw, lower jaw with one to three rows of conical

teeth; dentary teeth sometimes extending almost to symphysis. Small teeth on vomer head, palatine edentulous; ventral opercular membranes overlapping each other, posterior margin of opercle reaching base of pectoral fin rays. Interopercle, subopercle, preopercle and articular splintered, dorsal margin of opercle with some indentations; cirri on dorsal margin of epihyal and ceratohyal. Anal fin origin two to four rays in advance of dorsal fin origin, its end ca. one to two scales distance from caudal peduncle; dorsal fin end opposite to or immediately before anal fin end. Pelvic fin tip separated from anus by ca. four to six scales.

COLORATION IN ALCOHOL: Background pale; a brown band running along midline of body, from origin of pectoral to caudal peduncle. Seven to nine brown dorsal saddle marks, most of them connecting midline bar; a fine brown vertical line on caudal peduncle. Eyes with conspicuous striation radiating from the pupil opening (striae not found in some specimens); a black bar adjacent to the anterior and posterior openings of pupil, the one on the posterior side more pronounced. An interorbital black bar present in most specimens. Black, fine bands on caudal fin; dorsal fin rays with vestige of black pigmentation; cheeks, tip of snout and lower jaw with some black pigmentation.

DISTRIBUTION: L. polyactis was previously known only from the North Island, New Zealand. The two specimens from lot NMNZ 19885, however, were collected at the Chalky Is., Fiordland (South Island, New Zealand); this represents a considerable extension in the range of this species. See Fig. 3.

REMARKS: L. polyactis is one of the few creedid species for which some behavioral information exists. Nelson (1979) reported on a specimen from Island Bay kept in a tank. According to his observations, the fish buried itself in the sand with the head exposed; the eyes rotated fully forward and backward independently. Water was drawn through the mouth and opercles (which remained motionless) via a pumping action of the branchiostegal membranes.

Crystallodytes Fowler, 1923

Crystallodytes Fowler, 1923, Occasional Papers of the Bernice Pauahi Bishop Museum of Polynesian ethnology and natural history, 8 (7): 390 (Type-species: Crystallodytes cookei , by original designation).

DIAGNOSIS: Body naked, except for lateral line scales; posterior tip of mesopterygoid strongly curved up, slightly projected onto dorsal surface of eyeball; lateral line scales with an elongate anteriorly tapered central lobe.

DISTRIBUTION: Central Pacific, as far East as the Pitcairn Group; Easter Island. Fig. 4.

Two species: Crystalodytes cookei and C. pauciradiatus. Fig. 1E.

CITATIONS: Schultz in Schultz et al., 1960 : 275; Nelson, 1978 : 352, 363; springer, 1982 : 158; Nelson, 1985 : 283, 285, 291, 292; Nelson and Randall, 1985 : 403; Nelson, 1986 : 5.

KEY FOR CRYSTALLODYTES SPECIES

1a. Dorsal fin rays 36-39.....C. cookei Fowler

1b. Dorsal fin rays 30-32.....C. pauciradiatus Nelson and Randall

Crystallodytes cookei Fowler, 1923

Crystallodytes cookei Fowler, 1923, Occasional Papers of the Bernice Pauahi Bishop Museum of Polynesian Ethnology and Natural history, 8 (7) : 390 (Type locality : Laie Beach, Oahu). Holotype: BPBM 3400.

CITATIONS: Schultz in Schultz et al., 1960 : 275; Gosline, 1963 : 241; Nelson, 1978 : 352, 353, 363; Tinker, 1978 : 350; Nelson, 1979 : 274, 276, 277; Leis, 1982 : 166-173, 175-179; Springer, 1982 : 38, 39, 122; Nelson, 1985 : 283, 287-290; Nelson and Randall, 1985 : 403-409.

MATERIAL EXAMINED: ANSP 51517 (4), Malaekahau, Oahu, Hawaiian Islands; ANSP 82240 (1), Oahu, Waianae, Hawaiian Islands; BPBM 7908 (1), Oahu, Hawaiian

Islands; Moku Manu; BPBM 15246 (7, two C+S), Oahu, Hawaiian; Kanohe Bay; FMNH 63619 (43, two C+S), Hawaii; Oahu; Kahuhu; USNM 307831 (1 C+S), Phoenix Is., McKean Is., W side of island, in front of flagpole. Total number of specimens: 57.

DIAGNOSIS: Pelvic fin formula I,5; splintered opercle; 36-39 dorsal fin rays; 35-41 anal fin rays; 53-58 lateral line scales.

DESCRIPTION (30.8 - 41.8 mm SL): morphometrics and meristics are respectively given in Tables 17 and 3-6. Snout gradually sloping in dorsal profile. Upper jaw fleshy extension projecting well beyond lower jaw; maxilla extending beyond posterior margin of orbit, tip not notched; lower jaw with knob at symphysis and bordered by cirri; anterior nostril enclosed in a tube, posterior one pore-like; cheeks without scales; tongue free, longer than wider; lateral line scales elongate, not trilobed; lateral line with gradual slope at pectoral fin tip and reaching ventral profile only at final 1/5 of body length. No teeth on head of premaxilla; upper jaw posteriorly with two rows of conical teeth, anteriorly with a single row, ending well before symphysis; dentary with two irregular rows of conical teeth; anteriorly with a single row, sometimes extending almost to symphysis. Vomer with conical teeth, palatine edentulous; ventral opercular membranes overlapping each other, opercular flap reaching pectoral fin base. Dorsal and anal fin rays unbranched; anal fin origin one to three rays behind origin of dorsal, its end ca. two lateral line scales distance from caudal peduncle; dorsal fin end opposite anal fin . Pectoral and pelvic fin rays unbranched; articular, interopercle, subopercle and opercle splintered, no indentations on preopercle. No cirri on lower hyoid arch.

COLORATION IN ALCOHOL: background light brown, with ca. 10-11 brown dorsal saddle marks, alternating with some ligther, narrower ones; last two dorsal marks dorsally joining a brown bar running along midline of body, from pectoral fin origin to caudal peduncle. Vestige of brown pigmentation on lower and posterior margins of orbit. Brown speckles on occiput.

DISTRIBUTION: This species is known from scattered localities in the West and Central Pacific Ocean, as far East as the Pitcairn Group. See Fig. 4.

REMARKS: Two subspecies, Crystallodytes cookei cookei and Crystallodytes cookei endeburyensis have ben recognized by previous authors. The latter was established by Schultz (1943), to accommodate specimens from the Endebury Is., which had higher dorsal and anal fin rays counts.The two examined specimens of the nominal subspecies (from the Phoenix Is.) had higher dorsal and anal fin counts than the material from the Hawaiian Is., which may indicate the existence of two morphs (similar findings were reported by Nelson & Randall, 1985). The low number of specimens examined for the subspecies, and the fact that majority of the specimens obtained C. cookei are from a single locality (Hawaiian Is.) do not allow me to make any generalizations about the distribution of those characters. Therefore, the two subspecies will be recognized in my study, until more specimens can be examined.

Crystallodytes pauciradiatus Nelson and Randall, 1985

Crystallodytes pauciradiatus Nelson and Randall, 1985, Proc. Biol. Soc. Wash., 98 (2): 403, figs. 1-2. Type locality: Easter Island, off Ahu Akapu. Holotype: BPBM 6734.

MATERIAL EXAMINED: UAM0Z 5607 (2), Easter Is., East end of Anakena. Total number of specimens: 2.

DIAGNOSIS: 30-32 dorsal fin rays; opercle not splintered; lateral line scales not trilobed, with an elongate central lobe.

DESCRIPTION (29.5 - 66.3 mm SL): morphometrics and meristics are respectively given in Tables 18 and 3-6. Snout gradually sloping in dorsal profile; upper jaw fleshy extension projecting well beyond lower jaw; maxilla reaching or extending beyond posterior margin of orbit, tip not notched. Lower jaw with knob at symphysis and bordered by cirri; anterior nostril enclosed in a tube, posterior one pore-like. Cheeks without scales; tongue free, longer than wider; lateral line gradually descending at pectoral fin tip, and reaching ventral profile at last 1/5 of body length; lateral line scales elongate, not trilobed. No teeth on head of premaxilla; upper jaw with two irregular rows of conical teeth, ending well before symphysis; lower jaw with one row of conical teeth almost reaching symphysis. Vomer with a patch of a few conical teeth, palatine teeth absent.

Ventral opercular membranes overlapping each other, opercular flap reaching pectoral fin base; articular, subopercle and interopercle splintered; opercle and preopercle entire. No cirri on lower hyoid arch. Dorsal, anal, pectoral and pelvic rays unbranched; anal fin origin two to four rays in front of dorsal fin origin, its end ca. two lateral line scales distance from caudal peduncle.

COLORATION IN ALCOHOL: Background light brown, with ca. 10 brown dorsal saddle marks, alternating with some lighter, narrower ones; a brown band running along midline of body; vestige of brown pigmentation between posterior m rgin of orbit and preopercle; light brown speckles on occiput.

REMARKS: Nelson and Randall (1985) described this species based on its possesion of a lower number of dorsal fin rays and lateral line scales than C. cookei. The two species closely resemble one another in their external morphology. Interestingly, Nelson and Randall (1985) pointed out that the collections of C. pauciradiatus "consist primarily, if not exclusively, of females". Unfortunately, I could only obtain two specimens of that species (both female) and could not examine the matter in depth; further examination of this problem is necessary.

DISTRIBUTION: C. pauciradiatus is only known from the Easter Island. See Fig. 4.

Chalixodytes Schultz, 1943

Chalixodytes Schultz, 1943, United States National Museum Bulletin 180 : 261. Type-species: Chalixodytes tauensis, by original designation.

DIAGNOSIS: 36-41 dorsal fin rays; 13-17 short dorsal marks; body scales confined to lateral line, one predorsal row, and caudal peduncle region (few specimens with body almost completely scaled).

DISTRIBUTION: Indo-Pacific, as East as the Pitcairn Group. Fig. 4.

One species, Chalixodytes tauensis. Fig. 1F.

CITATIONS: Smith, 1956 : 889; Schultz in Schultz et al., 1960 : 275, 280; Nelson, in: Smith, 1961 : 736, 737; Nelson, 1978: 352, 362, 363; Springer, 1982 : 158; Nelson, 1985 : 285, 290-292; Nelson and Randall, 1985 : 408; Nelson, 1986 : 5.

Chalixodytes tauensis Schultz, 1943

Chalixodytes tauensis Schultz, 1943 : 263 , fig. 24. Type locality : Tau Island at Siulagi point. Holotype: USNM 116083.

Chalixodytes chamaleontoculis Smith, 1956, Ann. Mag. Nat. Hist. 12(9) : 890, fig. 1.

CITATIONS: Smith, 1956 : 889, 891, 892; Schultz in Schultz et al., 1960 : Nelson in Smith, 1961 : 737; Jones and Kumaran, 1967 : 9, 1980 : 508; Nelson, 1978 : 353, 362, 363; Springer, 1982 : 38, 122; Nelson, 1979 : 276; Nelson, 1984 : 407, 408.

MATERIAL EXAMINED: FMNH 44361 (3), Bikini Atoll, Namu Is.; FMNH 44362 (10), Rongerik Atoll, Bock Is.; BPBM 17745 (16, 2 C + S), Marshall Is.; BPBM 17652 (2), Palau Is.; BPBM 17025 (2), Pitcairn Is.; BPBM 13543 (3), Mangareva; ANSP 117242 (5), West Pacific, Saipan; ANSP 130673 (4), Cocos-Keeling Is., West Is., off N end, 12°07'50"S, 96°48'55"E; ANSP 130671 (14), Cocos- Keeling Is., North Keeling Is., 11°50'00"S, 96°49'30"E; USNM 284389 (1 C + S), Rotuma, N coast, off Ropuri (at about 10 o'clock position), 12°30'S, 177°05'E; WAM 26102.018 (3, 1 C+S), Christmas Is., 10°29'S, 105°40'E; WAM 26107.006 (2), Christmas Is., 10°29'S, 105°40'E; WAM 29018.012 (3), Christmas Is. 10°31'S, 105°40'E; ANSP 151598 (1), Aden, Gold Mohur Bay, 3 miles E of Steamer Point Harbour, 12°46'S, 44°59'E; ANSP 151597 (5), Arras Is., Amirantes-Three Cables W from SE corner of reef, 05°24'S, 53°13'E; BPBM 16281 (4), Reunion: Cap Houssaye; ROM 56634 (2), Comores, 12°11'09"S, 44°19'03"E; ROM 56635 (1), Comores, 12°11'09"S, 44°19'03"E; UAZM 5518 (2, C+S), Mauritius. Total number of specimens: 83.

DIAGNOSIS: Same as diagnosis of genus.

DESCRIPTION (28.5 - 45.1 mm SL): morphometrics and meristics are respectively given in Tables 19 and 3-6. Snout gradually sloping in dorsal profile; upper jaw fleshy

extension projecting well beyond lower jaw; maxilla extending beyond posterior margin of orbit, posterior tip not notched, concealed under skin fold. lower jaw with knob at symphysis and bordered by cirri; anterior nostril enclosed in a tube, posterior one pore-like; eyes dorsolateral, cheeks scaleless; tongue free, longer than wide, with pointed tip. Lateral line scales with central expanded lobe, not trilobed; lateral line with gradual slope at pectoral fin tip, posteriorly running parallel to ventral profile. In most specimens, the body is scaleless except for the lateral line, one row of predorsal scales, and scales in the caudal peduncle region. Premaxilla toothless, one to three rows of conical teeth on upper jaw; lower jaw with one to five rows of conical teeth, ending well before symphysis; vomerine teeth present, palatine edentulous; ventral opercular membranes overlapping each other, opercular flap reaching base of pectoral fin; Dorsal and anal fin rays unbranched; anal fin origin one ray in advance of dorsal fin origin, its end ca. two lateral line scales distance from caudal peduncle; dorsal fin end opposite anal fin. Pectoral and pelvic fin rays unbranched, pelvic fin tip slightly beyond pectoral fin base. Articular, subopercle and interopercle splintered, dorsal margin of opercle without indentations; no indentation on preopercle. No cirri on lower hyoid arch.

COLORATION IN ALCOHOL: Background pale; 13-17 short, brown saddle marks; vestigies of brown pigmentation immediatly behind the orbit. Schultz (1943) provides a more complete description of this species' coloration.

DISTRIBUTION: same as distribution of genus.

REMARKS: Schultz (1943) described C. tauensis based on 34 specimens collected at two localities in the Pacific Ocean. Later, Smith (1956) described C. chamaleontoculis based on a single specimen from the Indian Ocean. Smith correctly pointed out that the two species closely resembled one another, and stated that he only recognized them because of the "vast distance between the two localities." Later, Jones and Kumaran (1967) united the two species, but their justification was limited to "the differences between [the two species] are so slight that we unite the two." Nelson (1978) treated C. chamaleontoculis as a valid species, based on its "greater number of dorsal and anal fin rays and other slight differences". Interestingly, in that same paper, Nelson provisionally identified specimens from Cocos- Keeling Is., Indian Ocean (an intermediate location between the areas of occurence of the nominal species of Chalixodytes) as C. tauensis (which implies that dorsal and anal fin rays counts for those specimens were lower than in the Western Indian Ocean form). Springer (1982) noted that dorsal and anal fin rays counts of specimens from Christmas Island, Indian Ocean, were intermediate between the two species of Chalixodytes; he then stated that "it seems possible that the two species may only represent geographic populations of a single species". He, however, recognized the two species, because of the "extensive geographic gap between the two groups of populations, from which no specimens of Chalixodytes are known". This, according to him, could be an indicative of an effective barrier allowing the populations to diverge. Nelson and Randall (1985), in their key for Creediidae species, mentioned that "the two nominal species [of Chalixodytes] are poorly differentiated from one another and are only provisionally recognized here." My findings confirm that the boundaries between the two nominal species of Chalixodytes are ill-defined, and that the two diagnostic characters (number of dorsal and anal fin rays) for those taxa clearly overlap in the Cocos-Keeling and Christmas Is. area (as well as in other localities). Other characters that have been used to separate the two nominal species, such as number of dorsal saddle marks, number of lateral line scales,

also overlap throughout the species' distribution. Also, I could not find any osteological characters which clearly separate C. tauensis from C. chamaleontoculis. In my study, Chalixodytes chamaleontoculis is treated as a junior synonym of Chalixodytes tauensis (see below for comments on the P.C.A. results).

P.C.A. RESULTS:

The scatter plot from the P.C.A. is given in Fig. 10. The best discrimination between the two nominal species was obtained when the second component of the morphometrics dataset was plotted against the first component of the meristics dataset. However, the clusters separating the two nominal species showed overlap, even when the specimens were not from intermediate localities. As stated before, I could not find any osteological characters to separate the two taxa.

Apodocreedia de Beaufort, 1948

Apodocreedia de Beaufort, 1948, Transactions of the Royal Society of South Africa, 31: 476 (Type species: Apodocreedia vanderhorsti, by monotypy).

DIAGNOSIS: pelvic fin absent; posterior tip of mesopterygoid projected over dorsal side of eyeball; lateral line scales with elongate posterior extension; ascending processes of premaxillae fused together. This species can also characterized by the following characters: lateral line abruptly descending at pectoral fin tip, then running parallel to anal fin base, eight branched caudal fin rays.

DISTRIBUTION: Apodocreedia is known from relatively few localities in southeastern Africa. Fig. 4.

One species, Apodocreedia vanderhorsti. Fig. 1G.

Apodocreedia vanderhorsti de Beaufort, 1948

Apodocreedia vanderhorsti de Beaufort, 1848 : Transactions of Society of South Africa, 31 : 476, Fig. 1 (Type locality: Inhaca Island, Delagoa Bay, Mozambique).

CITATIONS: Schultz in Schulltz et al., 1960 : 274 as Apocreedia (sic); Smith, 1961: 174; Gosline, 1968 : 52 as Apocreedia (sic) ; Nelson, 1978 : 352, 353, 362; Nelson, 1979 : 276; Nelson and Randall, 1985 : 407; Nelson, 1986 : 736, in Smith and Heemstra (eds.).

MATERIAL EXAMINED: RUSI 9548 (15), Zululand : Boteler Point; RUSI 76-27 (20), Kwazulu : Sodwana Bay; RUSI 9054 (50), Kwazulu, Sodwana Bay; RUSI 76-21 (60, 5 C+S), Kwazulu: Reef 6.5 Km N of Island Rock; UAMZ, formerly RUSI 76-21, (3, C+S), Kwazulu: Reef 6.5 Km N of Island Rock. Total number of specimens: 148.

DIAGNOSIS: Same as diagnosis of genus.

DESCRIPTION (63.1 - 77.9 mm SL): morphometrics and meristics are respectively given in Tables 20 and 3-6. Snout gradually sloping in dorsal profile, upper jaw fleshy extension projected well beyond lower jaw; maxilla extending beyond posterior margin of orbit, tip not notched. Lower jaw with knob at symphysis and bordered by cirri; anterior nostril enclosed in a tube, posterior one pore-like. Cheeks without scales; tongue free, longer than wider; lateral line abruptly descending at pectoral fin tip, then running parallel to anal fin base; lateral line scales with elongate posterior extension. Head of premaxilla toothless; upper jaw with two incomplete rows of conical teeth, ending near premaxillary head; lower jaw with two to three rows of conical teeth. Vomer with conical teeth, few teeth on palatine. Ventral opercular membranes overlapping each other, opercular membranes reaching pectoral fin base; articular, subopercle, interopercle and dorsal margin of opercle splintered; no indentations on preopercle. No cirri on lower hyoid arch. Dorsal, anal and pectoral fin rays unbranched; anal fin origin ca. five to six rays behind dorsal fin origin, its end ca. two to three scales distance from caudal peduncle.

COLORATION IN ALCOHOL: background cream, with brown speckles on scale margins; brown speckles on occiput. Abdominal region golden in some specimens.

DISTRIBUTION: Same as distribution of genus.

REMARKS: Apodocreedia vanderhorsti is one of the most distinctive creediid species; the absence of the pelvic fin alone separates that monotypic genus from all other creediids;

Nelson (1985) indicated that the relationships between Apodocreedia, Crystallodytes and Chalixodytes were uncertain and that "Apodocreedia may very well be closer to Tewara cranwellae than are the species of the other genera."

VI. OSTEOLOGY OF THE CREEDIIDAE

This section encompasses a description of the osteology of the type-species of the type-genus of the Creediidae, Creedia haswelli, and compares that species with representatives of the remaining creediid genera. Illustrations are provided for the osteological features of this species and of Limnichthys fasciatus. I have chosen to illustrate the two aforementioned species because they have been thought to comprise "separate lineages" of creediids (Nelson, 1985), and have been used by some authors (see "historical review") to divide creediids into two subfamilies or families.

Some information on the comparative osteology of creediids can be found in Nelson (1985); however, the following account represents the first detailed comparative study of the entire skeletonof representatives of all creediid genera. Also, previous to my study, some parts of the skeleton of creediids had not been illustrated (e.g. branchial arches, ventral side of the skull). Illustrations are provided for the various regions of the skeleton of Creedia haswelli (based on AMS I. 9002) and Limnichthys fasciatus (based on UAMZ uncatalogued, Awakominato, Chiba, Japan) and are given in Figs. 12 - 24.

Skull (Figs. 13 A,B; 14 A,B)

The skull of C. haswelli is elongate and narrow, its maximum width (the distance between the pterotics) contained 2-2.5 times in its length. The interorbital area is very narrow, its least width contained ca. 15-16 times in the maximum distance between the pterotics. Most of skull elements, posterior to infraorbital area (both on the dorsal and ventral surfaces), overlap with their adjacent bones. The bones are smooth, covered by a layer of skin, and virtually devoid of crests. There are five relatively large orifices (the median one elliptic-shaped, the lateral ones rounded) on the anterodorsal surface of the frontals.

The remaining genera have a less elongate and posteriorly wider skull, its maximum width (at the level of the pterotics) contained 1.5-2 times in its length. In Schizochirus each frontal has one shallow, median orifice on the anterodorsal surface, one laterally placed, and two smaller ones on the anterolateral corner (posterior to the orbits). Two elliptic pores are present at the posterior tip of the interorbital bridge. Limnichthys has one or two rounded pores on the interorbital region (more posteriorly placed than the one in Schizochirus; each frontal also bears an anterolateral, rounded orifice (posterior to the orbit). In Tewara, each frontal has a comparatively large, rounded median orifice, and an anterolateral one about half the size of the median one. Each frontal bone of Crystallodytes has a median orifice (posterior to the orbit) and a slightly smaller one on the anterolateral surface. In Chalixodytes the orifices are similar to the ones found in Crystallodytes, but the median one is about the same size as the lateral one. In Apodocreedia, there are two anterolateral pores on each frontal, and a median one, at the level of the posterior margin of the orbit; the median pore is reduced in size, being ca. three times smaller than the lateral ones.

Ethmoid Region (Figs.13A,B, 14A,B; 15C, 16C) - The vomer has a broadened head with a rounded anterior margin and a tapered posterior strut; each side of the posteroventral margin of the head has a pointed posteriorly directed projection. The vomer abuts the head of the maxillae anteroventrally, the palatines lateroventrally, the lateral ethmoids dorsolaterally, and the mesethmoid dorsally. Posteriorly, the vomer is firmly attached to the parasphenoid. The posterolateral margin of the vomerine head bears 2-4 small canine-like teeth. The mesethmoid is rounded anteriorly, with a median protrusion on its dorsal surface; posteriorly, the bone is tapered, its tip being inserted between the anterior end of the frontals. Dorsomedially the mesethmoid bears a longitudinal, narrow ridge on the

posterior half of the bone, its posterior tip lying between the anterior end of the frontals. Dorsolaterally, the mesethmoid supports the nasal; ventrally it is firmly attached to the head of the vomer. The lateral ethmoids delimit the anterior margin of the orbits; each has moderately broad lateral projections about one third the length of the nasal, a median circular foramen and a posterior sharp tripartite process. Each lateral ethmoid contacts the mesethmoid medially, the lacrymal laterally, the palatine ventrolaterally, the mesopterygoid posteroventrally and the frontal posterodorsally. The nasals are elongate and tubular; each has an expanded triangular anterior end and extends from the anterior tip of the frontal to the head of the maxilla. They are supported by connective tissue, and loosely connect to the mesethmoid medially, the lateral ethmoid posterolaterally and the vomer and palatine ventrally.

The ethmoid region of Creedia haswelli differs from the one found in the other genera as follows: in Schizochirus the anterior margin of the vomerine head is blunt; laterally it is slightly concave and bears a cluster of conical teeth. The lateral ethmoid foramen is larger, the nasals have a rounded tip and bear a lateral flange. The mesethmoid is similar in shape, but the posterodorsal projection is smaller. The nasals greatly vary in shape among creediid genera: they are somewhat J-shaped (in Limnichthys and Crystallodytes) crescent-shaped (in Tewara), L-shaped (in Chalixodytes) and S-shaped (in Apodocreedia). The anterior tip of the nasal is rounded or slightly rounded in the aforementioned genera. Limnichthys, Chalixodytes, Crystallodytes and Apodocreedia lack the posteriorly directed vomerine projection, and all but Tewara possess a posterolateral projection on the dorsal surface of the vomer, (smallest in Apodocreedia) where the teeth are located. The number of vomerine teeth is usually low in creediids (between two and six teeth), but some specimens of Limnichthys fasciatus can have more than ten.

Orbital Region (Figs. 12; 13A; 14A; 15A; 16A; 17A; 18A) - Each orbit is delimited by the lateral ethmoid anteriorly, the frontal mid and posterodorsally, the parasphenoid ventrally, the sphenotic posteroventrally; the laminar mesopterygoid shelf forms the floor of the orbit. Two sclerotic ossicles support the eyeball; a basisphenoid is absent. The frontals are narrow anteriorly and expanded laterally behind the orbits; they make up approximately 50% of the dorsal surface of the skull. Anteriorly each frontal has a forked tip, which meets the posterior end of a nasal bone and contacts the posterior end of the respective lateral ethmoid. Posterodorsally (behind the orbit) the frontals partially overlap the parietals, supraocciptal, and sphenotics. Posteroventrally, the frontals contact a medially directed flange of the sphenotics. Immediately before the point where the frontals fan out, there is a single dorsal interorbital pore; the anterior margin of the broadened portion of the frontals has a ventrally directed shelf, which delimits the posterior margin of the orbit; two large dorsal pores are present on the broadened base of each frontal. The parasphenoid is elongate, narrow anteriorly, broadened medially and tapered posteriorly. Midposteriorly each side has a wing which contacts the prootic and pterosphenoid dorsolaterally; posteriorly, the parasphenoid partially overlaps the prootic and basioccipital. Midventrally, each side of the parasphenoid bears a pointed anteriorly directed process, at the base of the parasphenoid wing. Each infraorbital series consist of four canal bones: the lacrymal is the largest and somewhat triangular; anteriorly it articulates with the lateral ethmoid and partially covers the head of the maxilla; posteriorly, it has a short projection which loosely contacts the second infraorbital; the second infraorbital is elongate and tube-like; posteriorly, it is firmly attached to the third infraorbital; the third infraorbital is approximately of the same length as the second one along the orbital margin, but it possesses a ventral laminar shelf. A small, incomplete ring-like fourth infraorbital is firmly attached to the sphenotic. The sphenotics are paired canal bones, firmly attached to the

anterolateral surface of skull. Ventrally the bear a large flange which overlaps the part of the parasphenoid ascending wing.

In the other creediid genera the frontals do not bear an anterior shelf, and its anterior end is not forked or slightly forked; in Schizochirus each frontal bears two pores anterolaterally and two midanteriorly. There are two pores in the interorbital area of Schizochirus and some Limnichthys. The anteriorly directed pointed projection of the parasphenoid is shorter in Limnichthys, Tewara and Crystallodytes. The infraorbital series of Schizochirus considerably differs from the one found in C. haswelli and remaining creediids: the lacrymal has a transverse median groove and lacks the posteroventral projection; the second infraorbital is squarish, the third lacks the ventral shelf; the fourth is larger, cone-shaped and more loosely attached (the fourth infraorbital is also cone-shaped in Limnichthys and Tewara). In Limnichthys, Tewara, Chalixodytes, Crystallodytes and Apodocreedia the second infraorbital is smaller than in C. haswelli .

Otic Region (Figs. 13A,B; 14A,B) - The parietals are widely separated from one another, and form part of the dorsolateral surface of the skull. Anteriorly each is overlapped by the frontal; medially they overlap the supraoccipital; laterally each contacts the pterotic, and posteriorly the epiotic. The epiotics are widely separated from one another, and form part of the posterodorsal surface of the skull. Each epiotic contacts the parietals anteriorly, the supraoccipital medially, and the pterotic laterally; each epiotic has a shallow recess where the dorsal arm of the posttemporal attaches. The supraoccipital forms the dorsomedial area of the skull and bears a very small median crest on its posterior surface. The supraoccipital is overlapped by the frontals anteriorly and by the parietals laterally; it contacts the epiotics posterolaterally and slightly touches the suture along the anterior

margin of the exocciptal posteriorly. Each prootic is relatively large and has a median foramen. It comprises approximately one half of the lateroventral surface of the skull; it overlaps the parasphenoid anteriorly and medially; it is overlapped by the intercalar posteriorly; it also contacts the pterotic and sphenotic laterally. The posterior margin of the prootic comes very close to the anterior margin of the basiocciptal but there is no contact. The sphenotics are adjacent to the anterolateral surface of the skull; dorsally each sphenotic partially overlaps the frontal and parietal; ventrally each barely contacts the parasphenoid wing and prootic; posteroventrally the sphenotic contacts the prootic. The anterior head of the hyomandibula tightly fits into a notch located at the point of contact between the sphenotic and prootic. The pterotics are the posteriormost bones on the lateral surface of the skull; dorsally each has a canal-like structure that meets the canal of the lateral extrascapular; in lateral view, each contacts the sphenotic anterodorsally, slightly touches the parietals and contacts the outer margin of the epiotic medially; each pterotic also contacts the prootic, is partially overlapped by the intercalar ventrally, and contacts the exocciptal posteriorly. Each intercalar is roughly square in shape, and most of its flattened surface covers the adjacent bones. Anteriorly it partially overlaps the prootic, laterally the pterotic, and midposteriorly the basioccipital. A central area of the intercalar receives the ligament that connects the short ventral arm of the posttemporal to the skull.

Main differences: the degree of overlap between the supraoociptal and the parietals is markedly increased in Crystallodytes; the supraocciptal crest is reduced to a stub in Chalixodytes and is more triangular and pointed in Crystallodytes.

Basicranial Region (Figs. 13B; 14B) - The basiocciptal is roughly fan-shaped and forms the midposterior portion of the ventral surface of the skull. Anteriorly its broadened margin partially overlaps the parasphenoid; dorsally it meets the exocciptals; laterally it partially overlaps the intercalar; posteriorly the tapered basisphenoid provides the articular surface for the first vertebra. The exocciptals lie immediately dorsal to the posterior portion of the basisphenoid; in ventral view, each has a circular foramen on its outer margin. The exoccipitals contact the pterotic and intercalar anteriorly; dorsally they contact the epiotic. In Limnichthhys, Chalixodytes and Crystalodytes the midanterior margin of the basioccipital is notched; in the other genera it is like it is in C. haswelli..

Jaws (Figs. 12; 13C; 14C; 15B; 16B) - The premaxillae are elongate, their heads being widely separated from one another; each premaxilla has an elongate posteriorly directed ascending process which extends slightly beyond the anterior margin of the mesethmoid; the tip of the ascending process lies on a relatively large, roughly squarish cartilaginous area. Each premaxilla also has a conspicuous rounded articular process and a maxillary process (postmaxillary process of Pietsch, 1989). The maxillary process is relatively narrow and convex in dorsal profile. A cluster of approximately four to six large, canine-like teeth is present on the base of the articular process of each premaxilla; ca. 10-12 canine-like teeth, slightly smaller than the ones on the base of the articular process, are present along each maxillary process. The maxillae are rod-like, with an expanded head and a broadened forked posterior tip. The maxillary head has two anteriorly directed projections, which tightly articulate with the premaxillary articular process laterally and medially. Each maxilla also contacts the respective palatine anteriorly, the lacrymal dorsally, and the premaxilla posteroventraly; the anterior tip of the nasal bones contacts

the maxillary head laterally. The forked, posterior tip of the maxilla extends to the level of the second infraorbital. The dentaries are arrow-shaped, toothed, with an anterodorsal knob. The dorsal arm of the dentary is slightly smaller than the ventral one, and has a dorsally directed process on its posterior tip. The outer surface of each dentary has 2-3 pores anteroventrally and a shallow, relatively large pit anterodorsally. Each dentary bears approximately 25-31 canine-like teeth. The articulars consist of an anteriorly directed pointed process which fits between the arms of the dentary, a dorsal anteriorly directed pointed projection, a ventral shelf, and a posterodorsal projection, which receives the quadrate. Each articular has a membranous moderately splintered area along its ventral margin. The angulars are relatively small, tightly fitted between the posterior tip of the articular, the anterior margin of the interopercle and the ventral tip of the preopercle.

Main differences: teeth are absent from the base of the articular process of the premaxilla in all other creediid genera except Schizochirus (present in all Creedia species). Heads of the premaxillae are separated from one another in Schizochirus, and, to a lesser degree, in Limnichthys; in the remaining genera the premaxillary heads meet medially. The ascending processes of the premaxillae are fused together in Apodocreedia. The posterior end of the maxilla is not forked in the other creediids, except for Schizochirus. The process on the articular bone is slightly smaller in Limnichthys and Tewara, reduced to a stub in Apodocreedia and absent in Crystallodytes and Chalixodytes. The maxillary process is absent in the other genera, except for Schizochirus. There are more teeth on each premaxilla (between 23 and 50) and usually more teeth on the dentary (between 20 and 45) in the remaining genera.

Palatine Arch (Figs. 15A,C; 16A,C) - Each palatine is an elongate, curved bone; anteriorly it is tapered and posteriorly it is broadened, with a forked tip. It contacts the head of the respective maxilla anteriorly, is firmly attached to vomerine head projections midanteriorly, to the lateral ethmoid medially and to the mesopterygoid posteriorly. The anterior tip of the ectopterygoid lies in the angle formed by the forked posterior end of the palatine. About 6 or 7 small canine-like teeth are present on the posterior half of the palatine (palatine teeth were absent in one of the cleared and stained specimens). The ectopterygoids are rod-like with a fan-shaped tip. Anteriorly each ectopterygoid attaches to the outer arm of the forked posterior end of the palatine; posteroventrally its small triangular tip is firmly attached to the lower corner of the metapterygoid and barely touches the upper corner of the quadrate along its anterior margin. The ectopterygoid does not make contact with any other bones. The mesopterygoids are elongate, laminar, somewhat concave, with a forked anterior end, and a slightly upturned tapered tip; they support the eyeballs ventrally and posteriorly. Each mesopterygoid is firmly attached to the posterior projection of the vomer anteriorly, contacts the lateral ethmoid anterodorsally and the palatine laterally. The median and posterior regions of the mesopterygoids do not contact any bones. The metapterygoids are relatively large, somewhat triangular and with a small tranversal crest on the dorsal surface; each metaperygoid contacts the hyomandibula posterodorsally and the ectopterygoid anteriorly. The ventral margin of each mesopterygoid closely approaches the dorsal margin of the quadrate, but the two bones only contact through a narrow posterodorsal projection of the quadrate. The remaining of the dorsal surface of the quadrate and the ventral surface of the metapterygoid are separated by cartilage.

Main differences: The palatine is without teeth and without a forked posterior end in the other genera, except for Schizochirus. In Crystallodytes the palatine bears two crests;

Schizochirus has one medial crest; the head of the palatine is more perpendicular to the shaft of the bone in the other creediid genera. The metapterygoid crest is absent in Schizochirus, and it is most pronounced in Tewara and Limnichthys; the mesopterygoid tip is more upturned, partially enclosing the posterior margin of eyeball in Limnichthys Tewara and Chalixodytes; in Crystallodytes and Apodocreedia it extends farther up and projects onto the dorsal surface of the orbit. The triangular tip of the ectopterygoid is larger in all genera, especially in Schizochirus; the ectopterygoid rod is wider in Schizochirus. There is less contact between the ectopterygoids and the palatines in the remaining genera, except for Schizochirus.

Hyoid Arch (Figs. 13C; 14C; 21B,C,D; 22B,C,D) - Each hyomandibula is roughly rectangular and has three distinct heads along its dorsal margin; the anteriormost head ventrally bears a canal and tightly articulates with the sphenotic and pterotic; the median head tightly articulates with the pterotic and the posterior one tightly fits in an articular fossa on the anterovental surface of the opercle. Ventrally each hyomandibula is partially overlapped by the metapterygoid; posteriorly it partially covers the preopercle. The sympletics are somewhat elongate and triangular and tightly fitted into the inner surface of the quadrate. Dorsally each is separated from the hyomandibula by cartilage; posteriorly each partially overlaps the lower corner of the metapterygoid. The quadrates are triangular, with an elongate, dorsally directed posterior projection. Each contacts a small area of the metapterygoid dorsally, the articular ventrally and the sympletic midventrally. Each quadrate barely touches the ectopterygoid anteriorly, and abuts the preopercle posteriorly. Each hypohyal consists of a dorsal and a ventral element. The dorsal one is a somewhat triangular cap which lies on top of the larger ventral element; it contacts the basihyal midanteriorly and the basibranchial 1 midposteriorly. The ventral hypohyal has an elongate

posteriorly directed projection which is firmly attached to the ceratohyal; medially the bone contacts the basibranchial 1. The ceratohyals are elongate, slightly broadened on both ends, and have a small projection midventrally. Anteriorly each contacts the ventral hypohyal and it is separated from the dorsal hypohyal by cartilage. Ventrally each ceratohyal supports five branchiostegal rays; posteriorly each is attached to the epihyal via an elongate projection. The triangular epihyals contact the ceratohyal anteriorly and the interhyal posterodorsally; the posterior end of each epihyal tightly fits into a depression on the inner surface of the interopercle. Each epihyal supports two branchiostegal rays anteroventrally. The interhyals are dorsally directed relatively small and narrow bones; anteriorly each articulates with a small depression at the tip of the epihyal; each interhyal also contacts the inner surface of the interopercle medially and the preopercle posteriorly. There are seven branchiostegal rays attached via their anterior heads to the ceratohyal and epihyal. The first three are attached to the anteroventral suface of the ceratohyal; the fourth is ventrolaterally placed; it lies on a groove at the base of the ventral projection of the ceratohyal; branchiostegal ray 5 is ventrolaterally placed on the posterior end of the ceratohyal. Branchiostegal rays 6-7 are attached to the ventrolateral surface of the epihyal. The first two branchiostegal rays are slightly smaller than the other ones. The basihyal is thin and elongate, with a small cartilage attached to its anterior end. Posterolaterally the basihyal contacts the dorsal hypohyals. Posteriorly it contacts the basibranchial 2 via cartilage. The urohyal is rod-like anteriorly, laterally compressed and dorsoventrally expanded posteriorly. It extends from the level of second basibranchial to slightly beyond the anterior end of the ceratobranchial 5. The urohyal contacts two bones: anteroventrally its head articulates with the anterior end of the basibranchial 2 via small lateral projections. Anterodorsally it is attached to the left and right hypohyals via a ligament.

Main differences: In Schizochirus, the branchiostegal rays are wider, and the urohyal is anterolaterally expanded; the basihyal is posteriorly wider in Limnichthys, Tewara and

Schizochirus. The urohyal is anteriorly forked in Limnichthys, Tewara, Crystallodytes and Chalixodytes, and has a laterally expanded head in Apodocreedia. It is shorter in Limnichthys and Tewara, and dorsoventrally expanded in those two genera and Schizochirus; in Crystalllodytes and Apodocreedia the urohyal is tapered posteriorly. The anterior tip of that bone lies on the anterior end of basibranchial 2 in Schizochirus and Limnichthys, on the mid-portion of basibranchial 2 in Tewara, and on the posterior end of basibranchial 2 in Crystallodytes and Chalixodytes. In Apodocreedia, it lies on the anterior tip of basibranchial 3. In Limnichthys, hypobranchial 3 bears two anterolateral projections. The hypohyals of Crystallodytes and Chalixodytes are reduced in size. There are six branchiostegal rays on the ceratohyal and one on the epihyal in Crystallodytes, Chalixodytes and Apodocreedia.

Opercular apparatus (Figs. 12, 13C; 14C) - The bones of the opecular region of C. haswelli are thin and unsculptered; most of them are splintered along their free margins. The preopercle is a narrow, crescent-shaped bone, tightly fitted between the quadrate, metapterygoid and hyomandibula (along the anterior margin) and the interopercle and subopercle (along the posterior margin). Its dorsal surface bears a canal which is part of the acoutico-lateralis system. Some parts of the free margin of the preopercle are very faintly splintered. Each interopercle is roughly triangular; its ventral margin being the widest. It articulates anteriorly with the posterior margin of the preopercle, dorsally with the lower corner of the opercle and posteriorly with the anterior margin of the subopercle. The anterior margin of the interopercle has a very shallow notch, which receives the angular bone; its lower half is splintered. The subopercles are roughly rectangular, with a slightly concave anterior margin, which attaches to the posteroventral margin of the opercle. Anteroventrally each contacts the interopercle. Ca. 2/3 of the surface of the subopercles is

splintered. The opercles are triangular, their anterior margin the widest. Each contacts the preopercle anteriorly, the interopercle anteroventrally, and the subopercle ventrally. An articular fossa, which receives one head of the hyomandibula, is anteriorly placed on the ventral surface of the opercle. The free margin of the opercle is entire.

Main differences: The free margin of the preopercle of the remaining genera has no splintering (except in Schizochirus); the opercle is smaller in Apodocreedia and Crystallodytes and it is splintered in the former genera and in one of species of Crystallodytes (some splintering of the opercle was observed in a few C+S specimens of Limnichthys polyactis and L. fasciatus). The interopercular anterior notch is more pronounced in the remaining genera (except for Schizochirus).

Branchial Arches (Figs. 21A; 22A) - The four basibranchials consist of three bony and one cartilaginous elements, separated from each other via cartilage. Basibranchial 1 is the shortest of the three bony elements; its anterior end is wedged between the posterior ends of the basihyal and hypobranchial 1; basibranchial 2 is hour-glass shaped and slightly larger than basibranchial 1; basibranchial 3 is narrow and elongate; its tip lies between the hypobranchials 3. Basibranchial 4 is a small, cartilaginous element situated between the anterior tips of ceratobranchials 3 and 4. There are three pairs of hypobranchials: hypobranchial one is the largest; midanteriorly each contacts the anterior end of the basibranchial 2; posteriorly it is separated from the ceratobranchial 1 by cartilage. Hypobranchials 2 are about half the size of hypobranchial 1; anteriorly each is separated from the tip of the basibranchial 2 by cartilage; posteriorly it is separated from the anterior end of the ceratobranchial 2 by cartilage. Hypobranchials 3 are the smallest in the series; midanteriorly they contact the posterior end of the basibranchial 3; posteriorly they are

separated from the ceratobranchial 3 by cartilage. There are five pairs of ceratobranchials: ceratobranchials 1-4 are elongate, approximately of the same size, and articulate with their respective hypobranchials and epibranchials. Ceratohyals 5 are slightly smaller than ceratohyal 1-4 and bear about 3-4 rows of conical teeth on their antero and middorsal surface. The four pairs of epibranchials attach to their corresponding ceratobranchials; epibranchials 1 and 2 are approximately of the same size, have a medial process and articulate respectively with the anterior and posterior ends of the pharingobranchials 2. Epibranchials 3 are anteriorly broadened, smaller than the preceding ones and have a small process.on its upper corner Anteriorly each epibranchial 3 contacts pharingobranchials 3 and 4; epibranchials 4 are slightly longer and narrower than the others; anteriorly each articulates with pharyngobranchial 4. Pharyngobranchial 1 is absent; pharingobranchials 2 are relatively small toothed plates, which medially articulate with a projection of pharyngobranchial 3; pharyngobranchials 3 are the largest elements of the series, and bear numerous teeth along most of its surface, but none on the lateral projection; each articulates with the epibranchials 2 and 3. Pharyngobranchials 4 are about the same size as pharyngobranchial 2 and also bear conical teeth; each articulates with epibranchials 3 and 4. Toothplates with several conical sharp teeth are present along the inner surface of each ceratobranchial 1, outer and inner surfaces of ceratobranchials 2 and 3, and outer surface of ceratobranchials 4. The inner surface of hypobranchial 1 and the outer surface of hypobranchial 2 bear two small plates, similar to the ones found along the inner surface of ceratobranchials 1. Each epibranchial 1 bears two small plates with spiny teeth along their ventral surface; epibranchials 2 have a combination of larger, more flatenned plates and a few smaller ones along their dorsal surface; a single small plate is present along their ventral surface. Epibranchials 3 have larger flatenned plates along their outer and inner surfaces; they also bear a few smaller plates along their dorsal and ventral surfaces. each epibranchial 4 bears a small plate along its inner surface. The outer surface of

hypobranchials 1 and ceratobranchials 1 bear gill rakers, shaped as large flattened plates with short conical teeth.

Main differences - In Schizochirus, there is an incomplete row of enlarged teeth on the inner margin of ceratobranchial 5, the teeth on pharyngobranchials are larger and hypobranchial 3 is larger, with a more prominent dorsolateral projection. The conspicuous dorsolateral projection is also found in Limnichthys and Tewara. In the remaining genera, that projection begins to expand downward (Crystallodytes) and becomes much curved down (Chalixodytes and Apodocreedia). In Tewara there are less teeth on pharyngobranchial 3 and there is less contact between hypobranchial and basibranchal 3. In Chalixodytes, Crystallodytes and Apodocreedia, the contact between hypobranchial and basibranchial 3 is further diminished, most markedly in Apodocreedia. The three latter genera also have a more cartilaginous basibranchial 3 than the other creediids.

Axial skeleton (Figs. 12; 17C; 18C; 23A; 24A)

There are 41-43 vertebrae (excluding the urostyle), the first 14-16 being precaudal; the first caudal vertebra has a much larger haemal spine than the last precaudal. The neural spines of most vertebrae are of the same length, except for the one on the penultimate vertebra, which is much shorter than the preceding ones. Haemal spines become noticeable around vertebrae 8 or 9, and become greatly enlarged around vertebrae 15-17; the last haemal spine is wider than the preceding ones. 29-33 epipleural ribs are present from vertebrae 1; pleural ribs are absent. The first 15-17 ribs have a slightly expanded head, ar ventrally directed and larger than the following ones. The remaining ribs get progressively smaller and more posteriorly directed; most ribs are placed on the midline of the respective vertebrae; the last 3-4 ribs are greatly reduced in size. The only autogenous element of the hypural plates is the parhypural, the other elements being fused. A hypurapophysis is

absent. Two relatively elongate epurals are present, the epural 1 being the smallest; uroneurals are absent. There are eight or nine branched caudal rays.

There are 38 vertebrae in the clear and stained specimen of Schizochirus (Nelson, 1985 gives a range of 36-41, including the urostyle (J. S. Nelson, pers. comm.), the first 14 with wider neural spines; there are 12 precaudal vertebrae in that genus, its haemal spines longer, interdigitating with 1/4- 1/2 of pterygiophores. There are 28 ribs, starting from vertebra one, most of them placed low on the vertebrae. First 13 ribs wider, all posteriorly directed. Nine branched caudal rays are found in Schizochirus. In Limnichthys, there are 37 to 45 vertebrae, 21-27 spine- like ribs, without expanded head, the ones on caudal region smaller; 14-16 precaudal vertebrae are present, the caudal vertebrae bear an anteroventral projection. The two to five last neural spines are squarish, not spike-like, and the last neural spine is not reduced; the two to six last haemal spines laterally expanded. There are eight branched caudal rays.and one or two epurals in Limnichthys. Tewara has 50-53 vertebrae (Nelson, 1985 gives a range of 49-55), 14 being precaudal. The 21-22 ribs are spine-like, the four to five last neural spines are squarish, last neural spine not reduced; the four to five last haemal spines laterally expanded; the caudal vertebrae bear an anteroventral projection. Eight branched caudal rays and one epural are present. There are 50-58 vertebrae in Crystallodytes (Nelson, 1985 gives a range of 48-60), 24-25 being precaudal; the caudal vertebrae bear an anteroventral projection. The 45 ribs are spine-like, the haemal spines are shorter, and the last neural spine not reduced; eight branched caudal rays and one epural are found in Crystallodytes. Chalixodytes possesses 56- 59 vertebrae, 23-24 being precaudal; the caudal vertebrae bear an anteroventral projection; the 23 ribs are spine-like, the last neural spine is not reduced, and the haemal spines are shorter. Eight branched caudal rays and one epural are present in that genus.

There are 55-58 vertebrae in Apodocreedia, of which 23 are precaudal; anteroventally, the vetebrae bear a process, similar to the one found in Crystallodytes, Limnichthys, Tewara and Chalixodytes.The 41 to 42 ribs are spine-like, the four to six anteriormost neural spines are wider; there are eight branched caudal rays and one reduced epural.in Apodocreedia. In this genus, the dorsal and ventral hypural plates are partially fused together.

Dorsal and Anal Fins (12; 23B; 24B) - There are 12-15 dorsal pterygiophores with two elements (except for the last one which only has the proximal element) and supporting one unbranched ray; the first dorsal pterygiophore is inserted between neural spines 21 and 22; in two clear and stained specimens, it bears a dorsal anteriorly directed crest ; the remaining dorsal pterygiophores are elongate with an expanded head. The ventral end of each proximal element of the dorsal pterygiophores interdigitates with approximately 1/2-1/3 of the length of the respective neural spine. The dorsal rays are biserial, segmented and approximately of the same length, except for the last one, which is much smaller. The anal fin consists of 23 or 24 unbranched rays, supported by 22 or 23 pterygiophores (the first anal pterygiophore bears two ventral projections and supports two rays); there are four anal pterygiophores anterior to the first caudal vertebra. All anal pterygiophores but the last one consist of two elements (only the proximal element is present on the last one); all pterygiophores opposite the caudal vertebrae interdigitate with approximately 1/3-1/4 of the respective haemal spines. The anal rays are of the same length, except for the last one, which is much smaller.

Main differences: Schizochirus has 20 dorsal pterygiophores, the first one with laminar flanges both anteriorly and posteriorly to the main axis of the proximal

pterygiophore; the next 16 pterygiophores only have the posterior flange, the last three do not bear flanges. The medial element of the dorsal pterygiophore has an anteriorly directed projection which tightly fits between the anterior tips of the rays. The first dorsal pterygiophore is inserted between neural spines 14 and 15; all pterygiophores interdigitate with 1/4-1/3 of the length of the neural spines. The anal fin consists of 20 (in the C+S specimen) biserial, segmented branched rays, supported by 19 pterygiophores. All pterygiophores but the first one have flanges anterior and posterior to the main axis of the proximal element; the flanges become progressively smaller caudad; the anterior ones are flattened ventrally and articulate with the dorsal surface of the medial element of all but the last anal pterygiophore (which only possesses the proximal element). All anal pterygiophores interdigitate with 1/3-1/2 of the length of the respective haemal spines. The first four anal pterygiophores strongly converge to the last precaudal vertebra. There are 20-33 dorsal pterygiophores in Limnichthys, the first one being inserted between neural spines 11 and 12 or 13 and 14; it bears two small anteriorly directed stubs. The anal fin consists of 22-34 rays, supported by 21-33 pterygiophores; the first 6-7 pterygiophores slightly converge to the last precaudal vertebra. The dorsal fin of Tewara has 34-36 pterygiophores; the first one is inserted between neural spines 13 and 14 and bears a small stub. The anal fin consists of 36-39 rays supported by 35-38 pterygiophores. The first six anal pterygiophores slightly converge to the last precaudal vertebra. Crystallodytes has 30-39 dorsal pterygiophores, each supporting one ray. The first pterygiophore is inserted betweeen neural spines 16 and 17. Interdigitation between neural spines and dorsal pterygiophores mostly around vertebrae 45-48; after that point, the pterygiophores barely reach the neural spines. The anal fin consists of 35-40 rays, supported by 34-39 pterygiophores. In Chalixodytes there are 35-40 dorsal pterygiophores. The first one is inserted between neural spines 17 and 18; the anal fin consists of 36-40 rays, supported by 35-39 pterygiophores. The interdigitation between neural and haemal spines and respective

pterygiophores is limited to the tips of those elements or interdigitaton does not occur. Apodocreedia has 35-39 dorsal fin rays; the first pterygiophore is inserted between neural spines 14 and 15 or 16 and 17; the anal fin consists of 32-36 rays, supported by 31-35 pterygiophores. Both dorsal and anal pterygiophores are positioned more horizontally than in the other genera and only around vertebrae 39-41 a very limited interditation occurs between those elements and their respective neural and haemal spines.

Pectoral and Pelvic Girdles and Fins (Figs. 17B; 18B; 19A,B; 20A,B) - Each posttemporal is a flat, canal bone,with two dorsal anteriorly directed processes, which attach the pectoral girdle to the skull. The dorsal process is wider and larger than the ventral one; it attaches to the posterodorsal surface of th epiotic. The ventral arm is about 2/3 the length of the dorsal one and connects the intercalar via ligament. Anteriorly each posttemporal contacts the posterior end of the extrascapular canal. The posterior end of each posttemporal is partially overlapped by the supracleithrum. Each supracleithrum is a flat elongate bone which partially overlaps and firmly attaches to the dorsal surface of the cleithral ridge. The cleithra are somewhat L-shaped with a ridge along their outer surface; the dorsal end of each cleithrum has three spines: two are covered by the respective supracleithrum; the third is the smallest, posteriorly directed; ventrally, it contacts the scapula near the scapular foramen. A very small and narrow postcleithrum is loosely attached to the ventral surface of the radials. Each scapula and coracoid attach to the cleithral shelf; posteriorly each scapula is fused to radial 1, which supports 4-5 pectoral fin rays. Midanteriorly each scapula bears a relatively small foramen, not covered by the cleithrum. The coracoids are separated from the cleithrum by cartilage; both ends of each coracoid attaches to the cleithrum, but a small median area does not contact that bone.

Posteriorly the coracoids are fused to three radials, which support 8-10 pectoral fin rays. The four radials are partially fused to one another and to the respective scapula and coracoid, except for the third one, which is separated from the coracoid via cartilage. The basipterygia are separated from each other, are concave and form a bowl-shaped pelvis. Each basipterygium contacts the pectoral girdle via an anterolateral flange which is firmly attached to a ventrally directed cleithral projection. Laterally the basipterygia bear an anteroposterior shelf which possesses a small medially directed spine (pelvic spur) at its tip. The anterior margins of the basipterygia are joined by cartilage; a small cartilage joins the two basipterygia midposteriorly. One spine and four unbranched rays articulate with the posterior margin of each basipterygium.

In Schizochirus the ventral arm of posttemporal is about 1/2 the length of the dorsal one; the cleithra are less L-shaped (i.e. , straighter), the cleithral dorsal spines are less developed, the ventral spine being the largest; there are two postcleithra, the upper one rectangle-shaped, the lower one broader dorsally and tapered ventrally; the scapular foramen is larger, reaching the ventral surface of that bone; the radials are more separated from one another, 11/2 radials are fused to the scapula, the remaining half of the second radial only attaches to the third radial; radials 1and 2 support nine pectoral rays; the coracoid does not contact the third radial, but is fused to the fourth one; radials 3 and 4 support seven pectoral rays. The uppermost pectoral ray is splintlike and unbranched, the upper rays are shorter and narrower than the middle ones; most rays are branched and markely segmented. The basipterygia are larger, with the anterior margins meeting medially; a posteriorly directed process is present midposteriorly. One spine and five branched rays articulate with each basipterygium.The pelvic spur is more robust but shorter. The lower arm of the posttemporal of Limnichthys is ca. 1/2- 2/3 the length of dorsal one. The contact between coracoid and cleithrum is reduced, the contact being made via a sharp process (in some specimens, the process is absent); five to six rays articulate

with the coracoid, seven to nine with the scapula; postcleithra are absent. The basipterygia of L. polyactis possess a posteriorly directed process, which is not found in the other species of Limnichthys. A squarish projection connects the cleithrum to the respective basipterygium in L. polyactis and L. rendahli; ; the pelvic spur is longest in L. fasciatus . In L. nitidus, its is usually wider than in L. fasciatus, and longer than the one found in L. polyactis and L. rendahli;. One spine and five rays articulate with each basipterygium. In Tewara, the ventral arm of the posttemporal is ca. 1/3 the length of the upper one. The orifice between the coracoid and cleithrum is slightly larger; six rays articulate with radials 3 and 4; six articulate with radials 1 and 2; the cleithral shelf is confined to the upper half of that bone. As in C. haswelli, the pelvic spur is small; the basipterygia posteriorly bear a process . One spine and five rays articulate with each basipterygium. The ventral arm of the posttemporal of Crystallodytes is about 1/3 the length of the dorsal one; the scapular foramen is concealed by the cleithral shelf, the area separating the coracoid from the cleithrum is smaller; six rays articulate with radials 3 and 4, eight with radials 1 and 2. The cleithral shelf is confined to the upper alf of that bone. The pelvic spurs are large and meet medially. One spine and five rays articulate with each basipterygium. In Chalixodytes, the ventral arm of the posttemporal is about 1/3 the length of the dorsal one; five rays articulate with radials 3 and 4, seven with radials 1 and 2. The area separating the cleithrum from the coracoid is slightly larger. The cleithral shelf is confined to the upper half of that bone. One spine and four rays articulate with each basipterygium. The pelvic spur are larger and meet medially. The lower half of the supracleithrum is wide, the upper half tapered. The ventral arm of the posttemporal of Apodocreedia is about 1/4 the length of the dorsal one The degree of fusion between the cleithrum and coracoid and between the radials is greater; the cleithral shelf is rudimentary, confined to upper fourth of the bone. In this genus, the pectoral radials completely overlap one another and the pelvic fin is absent.

VII. PHYLOGENETIC ANALYSIS

Gosline (1963) and Nelson (1985, 1986) were the first authors to point out osteological characters that separate the Creediidae from other fish families. Nelson (1985), presented a list of characters which "support the view that the family is monophyletic and which distinguish creediids from all other fishes." A cladistic analysis of the Family Creediidae, however, had never been conducted, and, prior to this study, generic interelationships had only been briefly examined (Nelson, 1985).

In my study, a phylogenetic analysis was conducted in order to: 1) test the monophyly of the Creediidae; 2) establish the generic interrelationships; 3) attempt to resolve the trichotomy Percophidae-Trichonotidae-Creediidae.

Eleven trachinoid genera were used as outgroups. Since the monophyly of the Suborder Trachinoidei and some of its members has not been clearly established, my approach was to try to search for derived characters for both the outgroups and the ingroup. No synapomorphies were found to unite all the taxa examined (outgroups and ingroup). In this section, character number is given in bold square brackets **[]**.

Analysis of the dataset, consisting of 77 unordered characters, by PAUP 3.0S produced a single shortest cladogram, both by the heuristic - SPR and TBR branch-swapping algorithms used, and by the branch-and-bound search option. The cladogram has a length of 109 steps and consistency index of 0.78 (excluding uninformative characters). The data matrix and the minimum length cladogram are respectively shown in Table 21 and Fig. 11. Two additional cladograms with lengths of 110 steps were obtained when the branch-swapping algorithm NNI was used.They are discussed below and presented in Appendix 3 .The term cladogram, instead of tree, is used to refer to the branching diagrams presented in this study, since they contain no relative time axis or direct ancestry relationships, characteristics of phylogenetic trees (Wiley et al., 1991).

VII.1. OUTGROUP CHARACTERS

Four of the five pinguipedid genera (Pinguipes, Prolatilus, Parapercis and Pseudopercis) were used in the analysis. Kochichthys could not be included in this study, since no cleared and stained material was available. However, two out of the three characters thought to be derived for the Pinguipedidae are found in that genus (I. Rosa, in prep.). The proposed synapomorphies for the Pinguipedidae are from Rosa (1987, unpublished M.Sc. thesis). The character intercalar bone with projection **[1]**, could not be checked in Kochichthys.

The presence of an oblique crest on the hyomandibula of pinguipedids **[2]** was first noted by Gosline (1968). Crests on the hyomandibula occur in other fish families, such as Percophidae and some notothenioids, but the position of the one found in the pinguipedids is unique. Pietsch (1989) describes this character as follows: a conspicuous oblique crest of bone that extends from the dorsal tip of the preopercle to a posteriorly directed flange of the metapterygoid. Synapomorphy 3, sphenotic bone with an elongate process **[3]** was first observed by Regan (1913). In all pinguipedids the sphenotics are unusually long and laterally expanded.

Genus Champsodon, the sole representative of family Champsodontidae, has been included in the analysis due to its position relative to the Creediidae-Percophidae-Trichonotidae tricotomy in Pietsch's 1989 cladogram. It apparently forms a monophyletic group with the Chiasmodontidae (Pietsch, 1989). However, there are uncertainties regarding the phylogenetic position of the Champsodontidae (Joseph S. Nelson, pers. comm.). In my study, that taxon is defined by three autapomorphies: **[4]** ridged nasal bone; **[5]** rugose hypurapophysis and **[6]** infraorbital series reduced to three bones. Champsodontids and Creediids share a derived condition of the posttemporal bone in

which the lower arm of that bone does not reach the ventral surface of skull **[40]**. Based on the topology of the cladogram, that character state is interpreted as being homoplasiously derived for the Creediidae the Champsodontidae nodes. As stated in the methods section, the Champsodontidae was excluded from one of the PAUP runs, to see how its deletion would affect the previously obtained tree. After the removal of that taxon, a tree four steps shorter was produced. This was due not only to the removal of the three autapomorphies of the Champsodontidae, but also because it eliminated the aforementioned homoplasy [character 40] between that group and the Creediidae.

The Trichonotidae consists of six species (Nelson, 1986) of sand-divers and has been thought to be closely related to the Creediidae by various authors; its only genus, Trichonotus, was used as an outgroup. Three autapomorphies, hooked dentary bone **[7]**, stranded lens **[8]** and dentary with a fleshy tip **[9]** define that taxon. Based on the minimum length cladogram, derived states of the following characters are homoplasiously shared by the Trichonotidae and Creediiidae nodes: lower jaw bordered by cirri **[10]**, lower jaw with dorsal knob **[11]** and one or two epurals **[76]**. Trichonotus and the Crystallodytes-Chalixodytes-Apodocreedia clade share a homoplasious character **[77]**, which refers to the interdigitation between anal pterygiophores and their respective haemal spines. In all outgroups but the Trichonotidae and the aforementioned creediid genera, the anal pterygiophores and haemal spines interdigitate on both the anterior and posterior halves of body; in the Trichonotidae and the Crystallodytes-Chalixodytes-Apodocreedia branch, interdigitation only occurs posteriorly. Trichonotus also shares one derived character **[12]** with Hemerocoetes and Spinapsaron, which is reversed at the squamicreedia node. The Percophidae, as recognized by Nelson (1984), includes three subfamilies: Percophinae, Bembropinae and Hemerocoetinae (monophyly of the Percophidae, however, has never been established). A close relationship between the latter subfamily and the Creediidae has been suggested by Nelson (1985). Five genera of the

Hemerocoetinae (Squamicreedia, Enigmapercis, Spinapsaron, Hemerocoetes and Matsubaraea) were examined and used as outgroups. The five genera share two derived characters: maxillary process flattened **[19]** and 1st basibranchial with lateral projections **[20]**. The derived states of characters 19 and 20 are not found in the other subfamilies (M.K. Das, pers. comm.). Among the examined Hemerocoetinae, Hemerocoetes and Spinapsaron are the only ones to possess maxillary spines **[21]**. That condition is not found in any of the other outgroups or the ingroup, and is interpreted as derived for those two genera. Maxillary spines, however, are found in other hemerocoetines, and define a larger clade than the one formed by Hemerocoetes-Spinapsaron. Four synapomorphies unite hemerocoetines and creediids: hypurapophysis absent **[22]**, loss of pleural ribs **[23]**, branched caudal rays eight or nine **[24]** and no extrascapular bone on dorsal surface of skull **[25]**.

Character **[26]** refers to the length of the fleshy upper jaw extension. Of all outgroups, only Enigmapercis, Squamicreedia and Matsubaraea possess a soft fleshy pad, which in my analysis was coded as part of a transformation series with the condition found in most creediids. Genus Pinguipes (family Pinguipedidae) possesses a well developed conical snout, but distinct from the one found in the creediids (i.e., the structure was not interpreted as being homologous to the one found in creediids). For this reason, that character was coded as missing for Pinguipes, as well for the some other outgroups. Hemerocoetines, Limnichthys, Tewara, Crystallodytes and Chalixodytes share a derived character **[27]**, which is reversed in the Creedia-Schizochirus and the Apodocreedia clades. Spinopsaron and creediids share a homoplasous condition **[28]**, in which the last dorsal pterygiophore articulates with one ray. That genus and Matsubaraea further share a homoplasous character **[29]** with creediids, in which the last anal pterygiophore articulates with one ray.

Genus Hemerocoetes is unique among the outgroups in the loss of dorsal fin spines **[30]**, a condition shared with creediids, and interpreted as a homoplasy for the Hemerocoetes node. Character **[31]** refers to the shape of lateral line scales. Four states were identified for the character: scales not trilobed (state 0), which is found in all outgroups but Enigmapercis, Squamicreedia and Matsubaraea. In these genera, as well as in Schizochirus and Creedia, the scales (posterior to the pectoral fin posterior tip) are trilobed, the lateral lobes being pointed and the central one usually being short (state 1). In Limnichthys and Tewara, the central lobe becames much larger than the lateral ones, the latter being rounded (state 2); in Chalixodytes, Crystallodytes and Apodocreedia, the lateral lobes are further reduced and the scales are elongate, with a central expanded lobe (state 3). The derived state of character **[32]**, lower pectoral fin rays thickened, is homoplasiously shared by Enigmapercis, Squamicreedia, Matsubaraea and Schizochirus. Character **[46]**, neural spine of the penultimate vertebra modified as a stub, is shared by Hemerocoetinae, Schizochirus and Creedia and is reversed to the primitive state at the Limnichthys node.

VII.2. MONOPHYLY OF THE CREEDIIDAE

The following characters have been identified as synapomorphies for the family Creediidae. Characters marked by an asterisk have been previously identified as being exclusive to the Creediidae by Gosline (1963). Those marked by two asterisks have been identified as exclusive to the Creediidae by Nelson (1985).

I) pelvis cup-shaped** **[33]**. All outgroup taxa possess a flat pelvis. The concave pelvis is found in all creediid genera but Apodocreedia, in which the pelvic girdle has been lost. The cup-shaped pelvis is considered to be the derived state of that character.

II) pupil directed forward*[34]. The pupils are directed laterally in the outgroups; the condition found in the creediids is interpreted as a synapomorphy for that taxon.

III) upper side of cleithrum with spine on ventral surface * [35] None of the outgroups have the spine; its presence is viewed as being the derived state of that character.

IV) gill rakers present only on lower limb of gill arch [36]. All outgroups have gill rakers on both limbs of the gill arch. The loss of the gill rakers from the upper limb is interpreted as the derived state of that character.

V) pelvic spur medially directed **[37]. The conspicuous spur of most of the outgroups (the spur is stub-like in the Pinguipedidae), is anteriorly directed. It is medially directed in all creediids but Apodocreedia (Apodocreedia lacks the pelvic fin and its associated structures). The medially directed spine is thought to be synapomorphic for creediids.

VI) lateral line posteriorly running near the ventral margin of body.* [38]. The lateral line of all outgroups posteriorly runs mid-laterally in the body. The condition found in creediids is interpreted as derived.

VII) dentary bone not completely toothed [39]. Teeth are present along the entire oral surface of the dentary in all outgroups. The loss of teeth on the symphysis and on the posterior portion of the dentary is considered derived.

VIII) Lower arm of postemporal not reaching skull [40]. In all outgroups, except for the Champsodontidae, the ventral arm of the posttemporal either extends to the intercalar bone (pinguipedids and trichonotids) or reaches the ventral surface of the skull but does not extend to the intercalar (hemerocoetines). In all creediids, it is reduced in size and does not reach the skull. The size reduction is hypothesized to be the derived state of that character; its presence in the Champsodontidae is interpreted as a homoplasy.

IX) posterior tip of ectopterygoid fan-shaped **[41]. The small fan-shaped tip of the ectopterygoid is not found in any of the outgroups; its presence in creediids is considered to be derived.

X) anterior tip of urohyal on second or third basibranchial **[42]**. In all outgroups, the anterior tip of the urohyal lies on the first basibranchial. The state found in creediids is interpreted as derived.

XI) posterior tip of mesopterygoid reaching the posterior margin of orbit **[43]**. In trichonotids and percophids (the only outgroups which possesss a laminar mesopterygoid), the posterior tip of the mesopterygoid does not reach the posterior margin of orbit. The elongation of the mesopterygoid is interpreted as derived. This character is further developed in some creediid genera.

Creediids also share the derived condition of character **[28]**, which refers to the loss of spines on the dorsal fin. This condition is considered to be homoplasiously derived for the Creediidae and Hemerocoetes nodes. Character **[76]** is also interpreted as being homoplasiously derived for the Creediidae and the Trichonotidae.

VII.3. CREEDIIDAE-TRICHONOTIDAE-PERCOPHIDAE CLADE

The Trichonotidae, Hemerocoetinae and Creediidae form a monophyletic group, based on six synapomorphies (characters marked by an asterisk had been previously observed on the Creediidae by Gosline (1964), and subsequently extended to the Trichonotidae and Percophidae by Nelson (1985; 1986):

I) mesopterygoid forming floor of orbit ***[13]**. In the two aforementioned outgroup taxa and in the Creediidae, the laminar mesopterygoid supports the eyeball. This condition is not found in any of the other outgroups and is interpreted as derived.

II) dentary bone with an upturned posterior tip **[14]**. The dentary bone of the outgroup taxa, except for Trichonotidae and Hemerocoetinae, is straight; in those two taxa and the Creediidae it has an upturned, toothless posterior tip. The latter state is hypothesized to be derived.

III) ectopterygoid bone rod-like ***[15]**. In all outgroups but the Trichonotidae and Hemerocoetinae, the ectopterygoid is widened. In the two aforementioned outgroups and the Creediidae, that bone is rod-like. This state is interpreted as derived.

IV) procurrent rays not extending beyond the epurals **[16]**. The procurrent rays of all outgroups but the Trichonotidae and Hemerocoetinae extend beyond the epurals. In those two taxa plus the Creediidae, the number of epurals is reduced, and they never continue onto the caudal peduncle past the epurals. The reduction in the number of procurrent rays is interpreted as a synapomorphy for the Creediidae-Trichonotidae-Hemerocoetinae clade.

V) sympletic contacting most of the adjacent bones **[17]**. In the remaining outgroups, the sympletic is mostly free from the adjacent bones. The condition found in creediids, trichonotids and percophids is interpreted as derived.

VI) opercular membranes extending to pectoral fin base **[18]**. In the remaining outgroups, the opercular membranes are short, and do not reach the pectoral fin. The state shared by trichonotids, percophids and trichonotids is thought to be derived.

VII.4. GENERIC INTERRELATIONSHIPS

The genera Schizochirus and Creedia form a monophyletic group based on the following synapomorphies: I) vomer with posteroventral projection **[45]**. The vomer of the outgroups and the remaining creediid genera (except for Tewara) lack the projection. Its presence is interpreted as a synapomorphy for Schizochirus and Creedia, and as a

homoplasy for Tewara; II) anterior portion of the premaxilla with a patch of canine-like teeth **[44]**. The premaxillae of all outgroups are completely toothed, and the partial loss of teeth is considered to be derived. A further derived state of this character is found in remaining creediid genera, in which the anterior portion of the premaxilla is toothless. III) **[47]** anterior portion of ribs widened. In all outgroups and the remaining creediids, the ribs are thin and spine-like; the state found in Schizochirus and Creedia is thought to be derived; IV) **[48]** maxillary process present as a trace. In the outgroups, the maxillary process is well developed; in Schizochirus and Creedia there is only a trace of the process (state 1). The latter condition is interpreted as derived. A further derived state is found in the other creediids, in which the process is absent.

The remaining creediid genera share the following synapomorphies:

I) posterior tip of maxilla not broadened **[49]**. In Schizochirus and Creedia, as well as in the outgroups, the posterior end of the maxilla is broadened. This is interpreted as the primitive state for that character, the alternate state found in the remaining creediid genera (tip weakly broadened or rod-like) being derived.

II) anterior nostril enclosed in a tube **[50]**. In Schizochirus, Creedia and the outgroups, the anterior nostril is pore-like. In the other creediids, the nostril is enclosed in a tube. This is interpreted as the derived state.

III) ventral surface of caudal vertebrae without projection **[51]**. In Schizochirus, Creedia and the outgroups, the caudal vertebae do not bear a ventral projection, which is found the remaining creediids. The presence of the projection is interpreted as derived.

IV) second infraorbital bone ovoid **[52]**. In creediids (except for Schizochirus and Creedia and the outgroups), the second infraorbital is round and reduced in size. This is interpreted as the derived state for that character.

V) first dorsal pterygiophore without flange **[53]**. In Schizochirus, Creedia and the outgroups, the first dorsal pterygiophore bears a flange or a large projection. In the remaining creediids, there are only two (state 1) or two stubs (state 2).

VI) postcleithra absent **[54]**. There are two postcleithra in Schizochirus and the outgroups, and one in Creedia. The other creediid genera do not have a postcleithrum.

VII) lacrymal bone with an elongate posterior projection **[60]**. In Schizochirus, as well as in the outgroups, the lacrymal does not bear a posterior projection. Creedia has a small projection (state 1), which is further derived in the remaining genera. The presence of an elongate projection on the lacrymal (state 2) is interpreted as derived for those genera.

This clade also shares the derived state of character **[26]**. Its presence in the Creedia branch is interpreted as homoplasious. Four characters change to other apomorphic states at the Limnichthys-Tewara-Crystallodytes-Crystallodytes node: **[43]**, **[44]**, **[48]** and **[60]**. Character **[61]**, interpreted as a synapomorphy for this node, is reversed at the Tewara node.

The Limnichthys-Tewara node is defined by two synapomorphies: two to six last haemal spines squarish **[74]**, and two to four last neural spines broadened or squarish **[75]**. The two genera also share state 2 of character **[31]**.

Crystallodytes, Chalixodytes and Apodocreedia form a monophyletic group based on the following derived characters:

I) ten or more anal pterygiophores preceeding the first caudal vertebra **[58]**. In the other creediid genera and the outgroups, less than ten anal pterygiophores preceed the first caudal vertebra. The increase in number is interpreted as a synapomorphy for Crystallodytes, Chalixodytes and Apodocreedia.

II) projection on hypobranchial 3 pointing down. In the other genera and the outgroups that possess the projection, the projection points up. The alternate state is interpreted as derived.

The following characters are also shared by the aforementioned clade: short cleithral flange **[55]**. In Schizochirus, Creedia and Limnichthys, a cleithral flange is found along the entire surface of the bone. In the other genera, it is confined to the upper half of the bone (state 1) or present as a rudiment (state 2). The latter states are interpreted as derived for Crystallodytes, Chalixodytes and Apodocreedia . Their presence in Tewara is interpreted as a homoplasy. Tewara, Crystallodytes and Chalixodytes also share a homoplasy in state 1 of character **[56]**.

Chalixodytes and Apodocreedia are tought to form a monophyletic group, based on character **[62]**. The presence of the derived state of this character in Creedia is interpreted as a homoplasy, given the position of Creedia in the obtained cladogram.

VII.5. GENERIC AUTAPOMORPHIES

Characters **[63]**, **[64]** and **[65]** are considered to be autapomorphic for Schizochirus. In this genus, the nasal bone has a large lateral flange **[63]**, not found in the other genera (however, a small flange was in observed in Hemerecoetes). Character **[64]** is based on the presence of a median tranverse groove found in the lacrymal bone and character **[65]** is based on the presence of lateral flanges on the anal perygiophores. Creedia is defined by characters **[66]** and **[67]**, respectively, number of dorsal fin rays lower than 19 and cheeks with a pocket of embeded scales. Creedia can also be characterized by state 1 of characters **[54]**, postcleithrum rudimentary and **[60]**, lacrymal with a small posterior projection. Limnichthys is a poorly defined genus, being characterized by state 1 of characters **[53]** and **[56]**. Tewara is defined by character **[68]**, which refers to the size of the central frontal pore. In that genus, the central frontal pore is much larger than the lateral ones. Crystallodytes is defined by character **[69]**.

In Crystallodytes, body scales are confined to the lateral line. Chalixodytes is characterized by the presence of a distally tapered supracleithrum **[70]**. The supracleithrum of Limnichthys fasciatus is also tapered, but both distally and proximally; the shape of the one found in Chalixodytes is unique. Apodocreedia is defined by characters **[57]**, **[71]** and **[72]** and by state 4 of character **[42]** and by state 3 of characters **[43]** and **[57]**.

VII.6 - THE TWO 110-STEP CLADOGRAMS:

As stated above, two additional trees, one step longer than the one found by two branch-swapping algorithms (heuristic search) and by the branch-and-bound search option were found.

The algorithms used in the heuristic search option are, in order of increasing effectiveness (Swofford, 1991): NNI (nearest neighbor interchange), SPR (subtree prunning-regrafting) and TBR (tree bisection-reconnection). The two 110 step cladograms were obtained when the NNI option was used.

Regarding the ingroup, the only difference between the 109 and 110 steps cladograms refers to the Crystallodytes-Chalixodytes-Apodocreedia node; in one of the two 110 step cladograms Crystallodytes and Apodocreedia (not Chalixodytes and Apodocreedia) formed a monophyletic group. The position of the other members of the ingroup was not changed.

The outgroup relationships, however, considerably changed in the 110 steps cladograms. Both of them grouped all the examined hemerocoetines and showed the Trichonotidae as the closest relative of the Creediidae.

Since both the most effective algorithms of the heuristic search and the branch-and-bound methods produced the same 109 steps cladogram, the phylogenetic hypothesis

presented in it was accepted as the most parsimonious solution given the dataset. However, the two slightly longer trees indicate that the hypothesis of sister group relationship between the Hemerocoetinae and Creediids should be viewed as very provisional. Once the monophyly (or not) of the Percophidae is established and the generic interrelationships of the percophid fishes are better understood, the aforementioned hypothesis should be re-examined.

VIII. GENERAL DISCUSSION

VIII. 1. CREEDIID SPECIES

Fourteen of the 16 nominal species of Creediidae are recognized as valid: Schizochirus insolens, Creedia haswelli, C. alleni, C. bilineatus, C. partimsquamigera, Tewara cranwellae, Limnichthys fasciatus, L. nitidus, L. polyactis, L. rendahli, Crystallodytes cookei, C. pauciradiatus, Chalixodytes tauensis and Apodocreedia vanderhorsti. Chalixodytes chamaleontoculis is considered to be a junior synonym of Chalixodytes tauensis and Limnichthys donaldsoni is treated as a junior synonym of Limnichthys nitidus. Two subspecies of L. nitidus are provisionally recognized. The Central Pacific specimens, grouped as L. nitidus donaldsoni, seem to have a distinctive color pattern from the Indian Ocean specimens, grouped as L. nitidus nitidus. The apparent color difference and disjunct distribution of the two forms served as the basis for the recognition of the two subspecies. Recognition of subspecies, however, is a problematic procedure in taxonomic studies, and should only be used as a classificatory device (Mayr and Ashlock, 1991). As pointed out by those authors, four aspects reduce the usefulness of that category: 1) the tendency of different characters to show independent trends of geographic variation; 2) the independent ocurrence of similar or indistiguishable populations in geographically separated areas; 3) the occurrence of microgeographic races within formally recognized subspecies; 4) the arbitrariness of the degree of distinction considered by different specialists as justifying separation of slightly differentiated populations. As stated above, the two subspecies of L. nitidus are only provisionally recognized, until the observed patterns of variation are better understood. Schizochirus insolens is a very distinctive creediid, by being deeper bodied than the other creediids, and it externally resembles some members of the Hemerocoetinae. However, it shares several

apomorphic characters with the Creediidae, and the family is hypothesized to be only monophyletic with its inclusion.

Creedia haswelli and C. alleni are morphologically more similar to one another than to the other two species placed in that genus. They share a unique condition in the lateral line scales, in which the central lobe is bordered by cirri-like projections. A new diagnostic feature was found for C. partimsquamigera: in this species, there are two rows of small embeded scales from the lower margin of the pectoral fin base to the the origin of the pelvic fin. Previous accounts of C. partimsquamigera (Nelson, 1983) described the anterior portion of the body of that species as completely scaleless (except for the lateral line scales). C. bilineatus is deeper bodied than the other Creedia species and can be characterized as having a pointed tongue (pointed tongues, however are found in the other creediid species, except for S. insolens).

Tewara cranwellae externally resembles some species of Limnichthys (see below), but can be separated from them based on the higher number of dorsal and anal fin rays (however, this character state is not exclusive to T. cranwellae).

Limnichthys fasciatus and L. nitidus are morphologically very similar to one another, and are best separated when coloration is available. However, there are some osteological characters which support the recognition of the two species; all but one examined specimens of L. fasciatus (USNM 285851) possess two epurals, whereas L. nitidus has only one. Also, the projection on the dorsal margin of the articular, present in L. fasciatus seems to be absent in L. nitidus. The latter species usually has a wide, shorter pelvic spur than L. fasciatus. The subspecies L. fasciatus major is not recognized as a valid taxon.

L. polyactis and L. rendahli, the two New Zealand species of Limnichthys, are morphologically similar to one another, but can be separated by the number of epurals, the width of the last neural spines (both characters first noted by Nelson, 1979) and the length

of the projection on the articular. L. polyactis and L. rendahli resemble Tewara in their external morphology. L. polyactis was previously known only from the North Island , New Zealand (Nelson, 1978). However, that species also occurs off the South Island, where L. rendahli is also found.

Crystallodytes cookei can be separated from its congener, C. pauciradiatus , by having a splintered opercle and a higher number of dorsal fin rays. Nelson and Randall (1985) noted that most, if not all specimens of C. pauciradiatus consisted of females, and this problem should be further examined.

Chalixodytes tauensis is widely distributed in the Indo-Pacific. It externally resembles Crystallodytes, but species in the two genera can be separated by the number of pelvic fin rays (five in Crystallodytes, four in Chalixodytes). Two species were formerly recognized in the genus Chalixodytes: C. tauensis and C. chamaleontoculis. The two species had been previously synonymized by Jones and Kumaran (1967), but were treated as valid by Nelson (1978) and Springer (1982). Nelson and Randall (1985), however, remarked that the two species were poorly differentiated from one another and were only provisionally recognized. My findings support the the synonymy proposed by Jones and Kumaran (1967).

Apodocreedia vanderhorsti is a very distinctive creediid species, with its loss of the pelvic fin. It externally resembles Crystallodytes and Chalixodytes, but does not have the dorsal marks found in the other two genera.

VIII.2. CREEDIID GENERA:

The seven genera recognized by Nelson (1984) are also validated in my analysis.

Schizochirus, a monotypic genus, is characterized by three autapomorphies (anal pterygiophores with flanges, lacrymal with transverse groove and nasal bone with lateral flange). Schizochirus and Creedia are hypothesized to form a monophyletic group which is the sister-taxon to the remaining creediid genera. This result differs from most previous classifications proposed for creediids, in which Schizochirus and Creedia were usually placed in separate groups. Nelson (1985): 291, Fig. 7 placed Schizochirus and Creedia in a single group. In his discussion, however, he considered Schizochirus to be the most primitive Creediid genus, and indicated that Creedia formed a separate lineage, characterized by the reduced number of dorsal fin rays. In my analysis, the reduced number of dorsal fin rays was interpreted as a synpomorphy for the four species of Creedia, and as such uninformative for establishing phylogenetic relationships. The two synapomorphies uniting Schizochirus and Creedia are the presence of a posteroventral projection on the vomer, which is also found in Tewara and interpreted as a homoplasy for that genus, and the anterior portion of the ribs widened. The two genera also share intermediate states of the characters referring to the mesopterygoid tip, the premaxillary teeth and the maxillary process.

Limnichthys, Tewara, Crystallodytes, Chalixodytes and Apodocreedia possess a number of synapomorphies (such as anterior nostril enclosed in a tube, round second infraorbital, no postcleithrum, etc) and are recognized as a monophyletic group. This clade is well supported, but, as discussed below, some of the clades within it are not.

Limnichthys is a poorly defined taxon, and its boundaries should be further delimited. The genus is identified by the intermediate stages of characters referring to the flange on the first dorsal pterygiophore and the ascending process of premaxilla. Further examination of that node is still necessary. Limnichthys and Tewara are hypothesized to form a monophyletic group, based on the presence of two synapomorphies: two to six last

neural spines widened or squarish, and two to four last haemal spines widened or squarish.

The clade formed by Crystallodytes, Chalixodytes and Apodocreedia is well supported by three derived characters (ten or more anal pterygiophores preceeding the first caudal vertebra, a downward projection on hypobranchial 3 and interdigitation between anal pterygiophores and haemal spines limited to the posterior region of body); the three genera also share intermediate apomorphic states of three characters.Within that clade, Crystallodytes is defined by the body scales confined to the lateral line, Chalixodytes by a dorsally tapered supracleithrum and Apodocreedia by (among other autapomorphies) the loss of the pelvic fin and the partial fusion of the dorsal and ventral hypural plates.

The clade formed by Chalixodytes and Apodocreedia is weakly supported and should be further examined. A single synapomorphy, urohyal short, was found for that node. The derived state of that character is also found in Creedia and was interpreted (based on the topology of the cladogram) as homoplasious for that node.

The minimum length cladogram obtained in my analysis represents a working hypothesis of the creediid generic interrelationships. Further work is still necessary to improve its resolution, especially at the Limnichthys-Tewara and Chalixodytes-Apodocreedia nodes.

VIII.3. MONOPHYLY OF THE CREEDIIDAE:

Creediids form a morphologically distinct group, defined by several synapomorphic characters. An analysis of 77 characters of taxonomic significance has demonstrated that the monophyly of the group is well-substantiated. Some of the characters used in my study had been previously observed by Gosline (1963) and Nelson (1985), and they have been shown to be valid synapomorphies for the Creediidae. A few characters indicated by

Nelson (1985), however, were useful at a higher level of generality (e.g. one set of epipleural ribs only; upper jaw fleshy extension) and were used to examine interrelationships of the family Creediidae. Synapomorphies for the Creediidae include pelvis cup-shaped, eye protruding, dorsal tip of cleithrum with spine fused to its ventral surface, gill rakers only present on the lower limb of gill arches, pelvic spur medially directed, etc.

VIII. 4. INTERRELATIONSHIPS OF THE CREEDIIDAE:

The clade formed by creediids-trichonotids and percophids is well supported by a number of synapomorphic characters. Four new derived characters, besides the two indicated by Nelson (1985), define that clade. The new synapomorphies are: posterior end of dentary upturned, procurrent rays not extending beyond the the level of the epurals, sympletic contacting most adjacent bones and opercular membranes reaching pectoral fin base. According to the obtained cladogram, sister-group relationship for the Creediidae lies within the Hemerocoetinae. However, until the monophyly of the Percophidae is established and a better delimitation of hemerocoetinae is achieved, that hypothesis is very provisional. A systematic study of all so-called percophid genera is much needed, not only to better delimit that family, but also to improve higher classificatory schemes.

VIII. 5. SUBORDER TRACHINOIDEI:

Although a thorough examination of the suborder Trachinoidei was not conducted in my study, a few considerations can be made, based on the examined material. The

suborder, as presently defined, is probably not a monophyletic group. If the characters postulated as derived for that assemblage by Pietsch (1989) are correct, the Opistognathidae, currently placed in the Suborder Percoidei, should be included in the trachinoids, as it possesses a pelvic spur.The character pelvic spur, however, seems to have a broader distribution than the suborder Trachinoidei, being found (at least) in some notothenioid families.

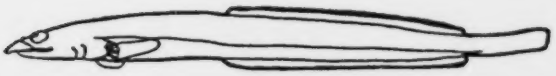
FIG. 1. Diagrammatic representation of the seven genera of the Creediidae: A) Schizochirus; B) Creedia ; C) Limnichthys; D) Tewara; E) Crystallodytes; F) Chalixodytes; G) Apodocreedia .

A

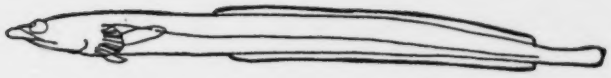
B

C

D



E



F

G

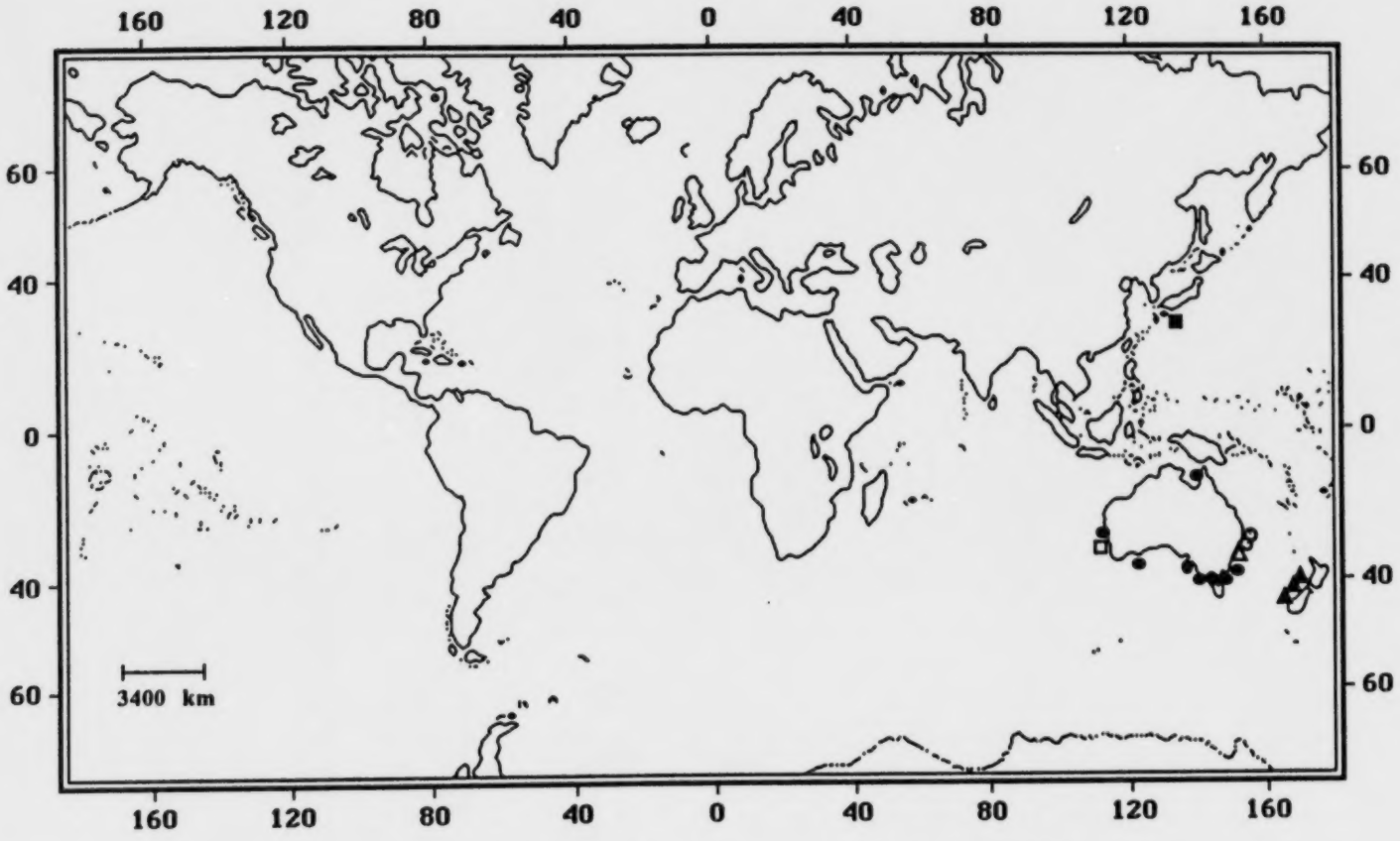


FIG. 2 .- Geographic distribution of Schizochirus insolens (o) , Creedia haswelli (•), C. alleni (□), C. partimsquamigera (△) , C. bilineatus (■) and Tewara cranwellae (▲) based on the examined material.

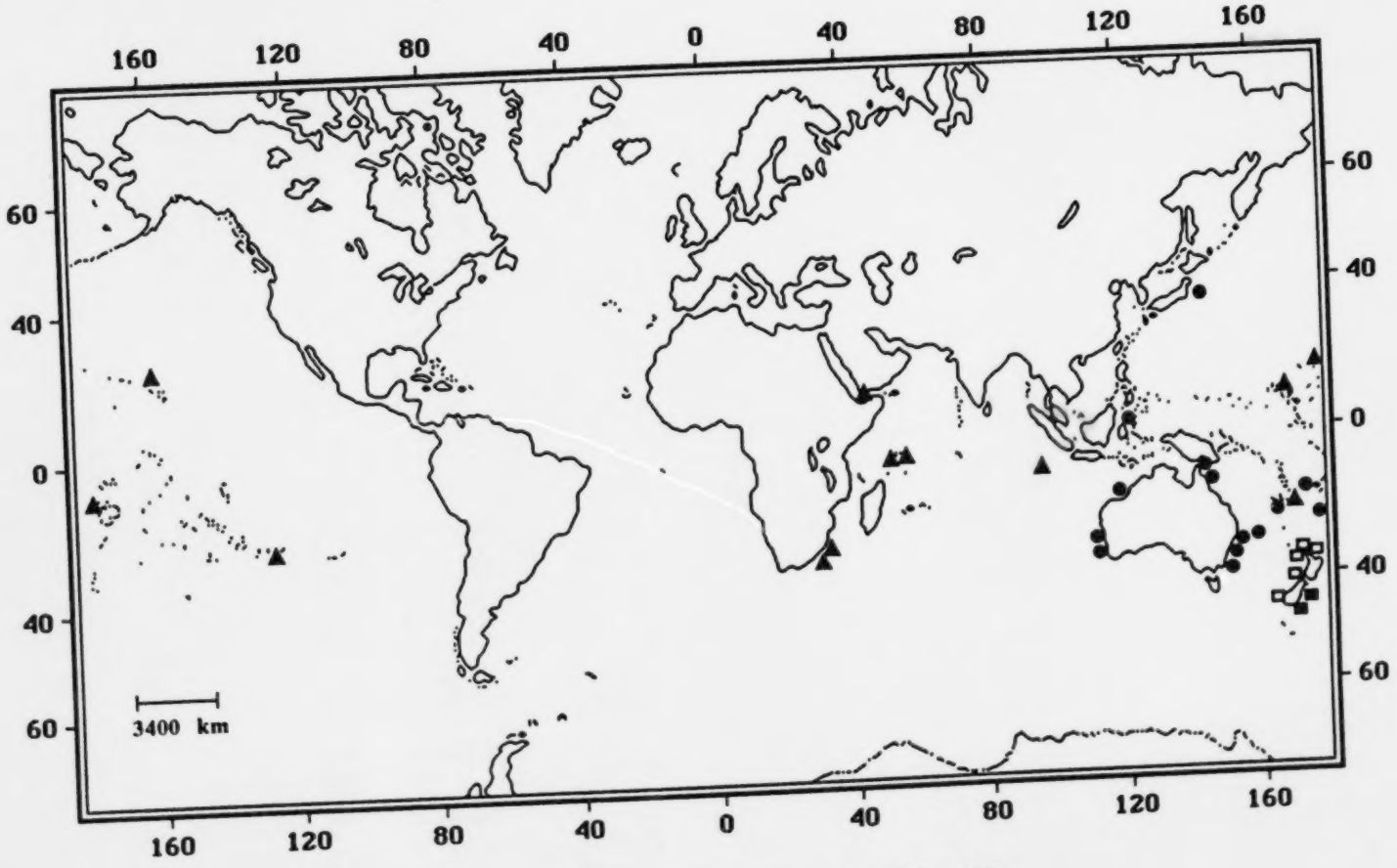


FIG. 3 .- Geographic distribution of Limnichthys fasciatus (●), L. nitidus (▲), L. polyactis (▫) and L. rendahli (■) based on the examined material.

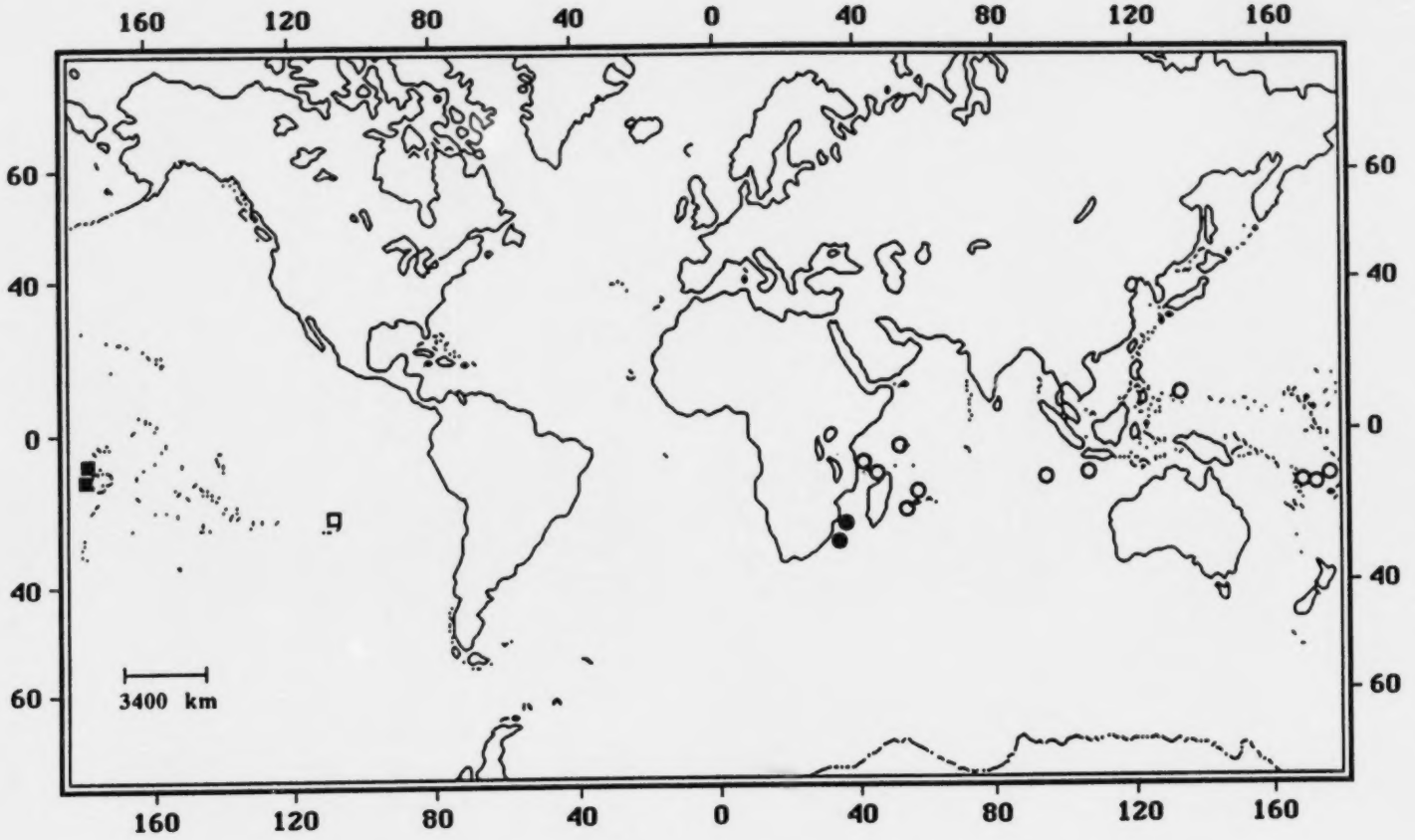
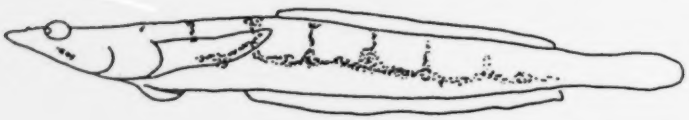


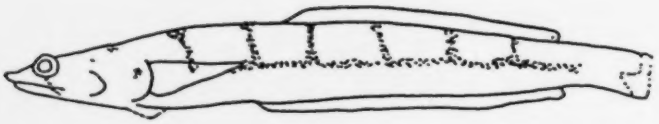
FIG. 4 .- Geographic distribution of Chalixodytes tauensis (○), Crytallodytes cookei (■), Crystallodytes pauciradiatus (□) and Apodocreedia vanderhorsti (●) based on the examined material.

FIG. 5, A-D. Diagrammatic representation of the various color patterns observed in preserved specimens of Limnichthys fasciatus.



A

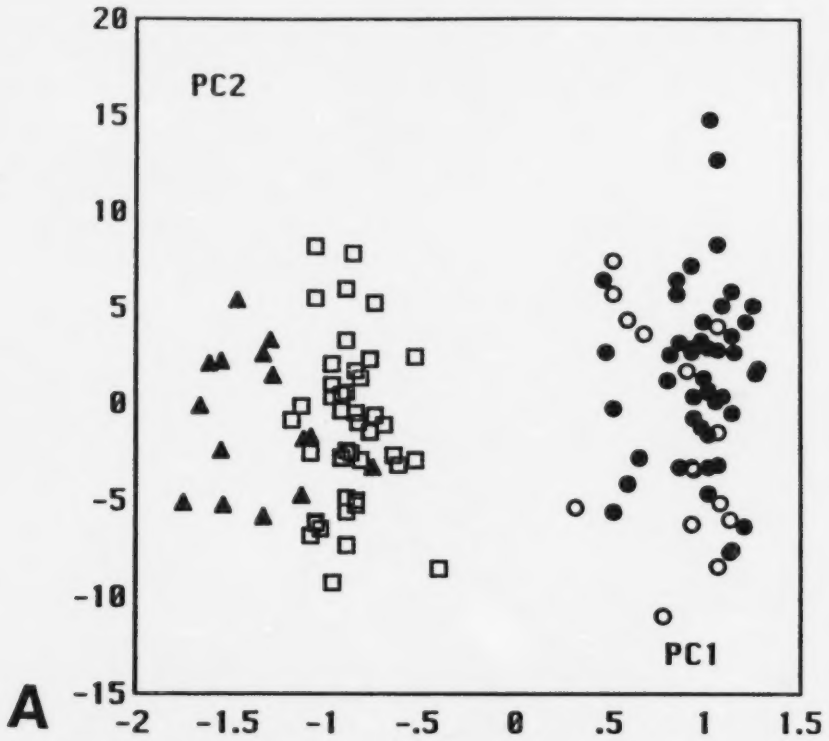
B



C

D

FIG. 6. Principal components analysis of three species of Limnichthys: L. fasciatus (solid circles; the Fijian specimens shown as open circles), L. nitidus (open squares) and L. donaldsoni . Scatter of Component I of the meristic dataset, including color (PC1) and Component II of the morphometric dataset (PC2); B)Scatter of Component I of the meristic dataset, excluding color (PC1) and Component II of the morphometric dataset (PC2).


PC2
PC1
20
15
10
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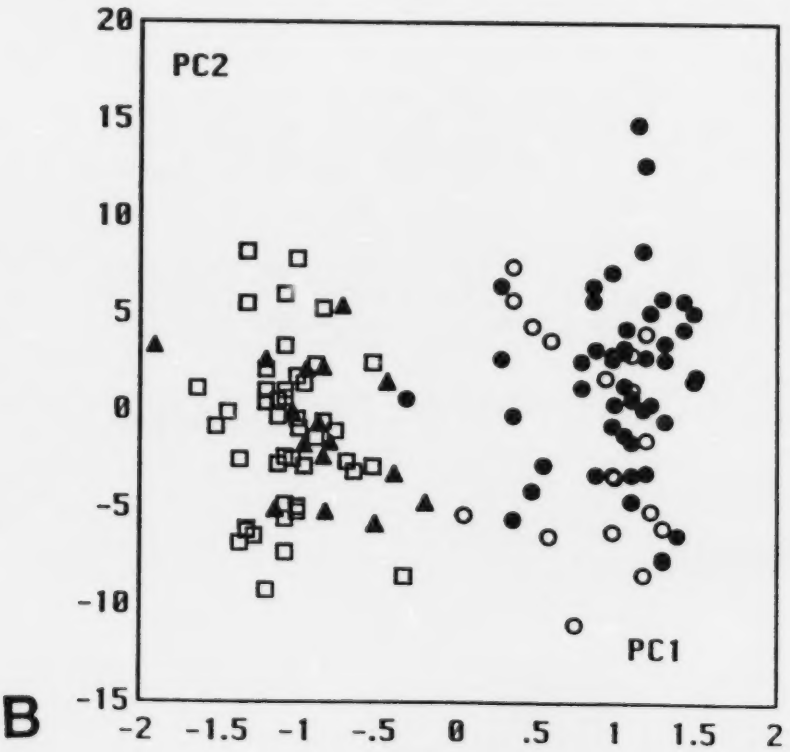
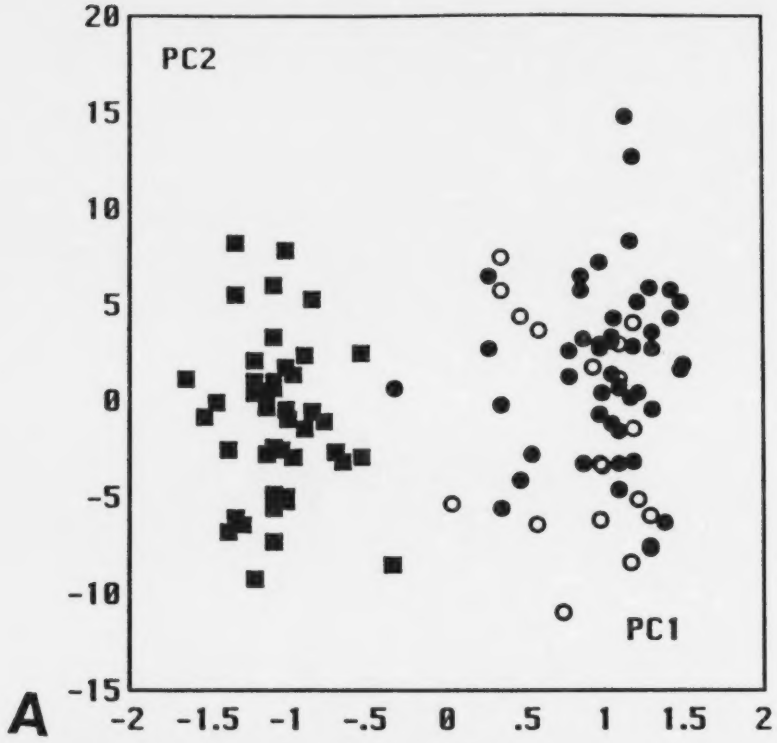
0
-5
-10
-15
-2
-1.5
-1
-.5
0
.5
1
1.5

A


PC2
PC1
20
15
10
5
0
-5
-10
-15
-2
-1.5
-1
-.5
0
.5
1
1.5
2

B

FIG. 7. Principal components analysis of two species of Limnichthys: L. fasciatus (solid circles; the Fijian specimens shown as open circles), L. nitidus (solid/open squares) A) Scatter of Component I of the meristic dataset, excluding color (PC1) and Component II of the morphometric dataset (PC2); B) Scatter of Component I of the meristic dataset, including color (PC1) and Component II of the morphometric dataset (PC2).


PC2
PC1
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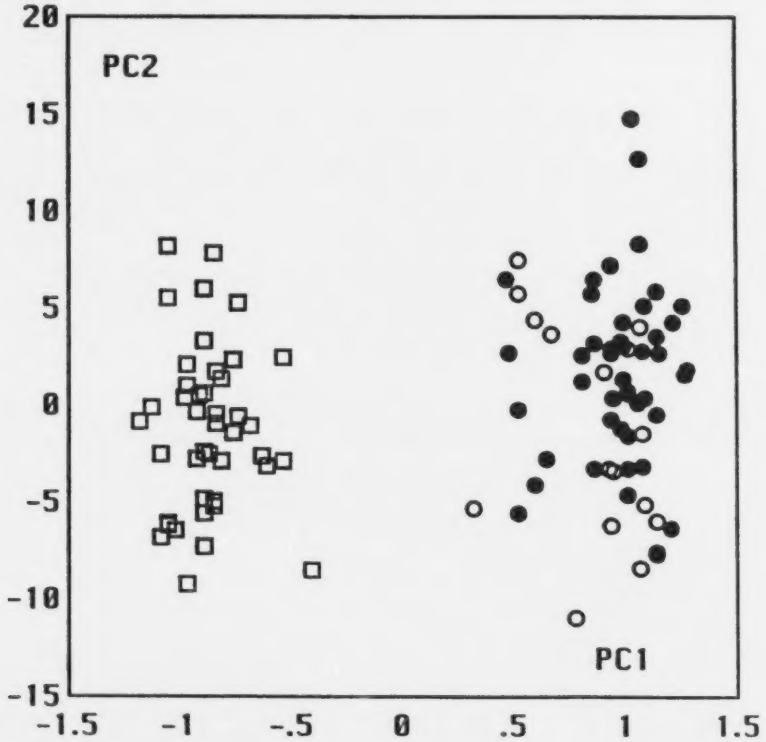
1.5
2

A


PC2
PC1
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15
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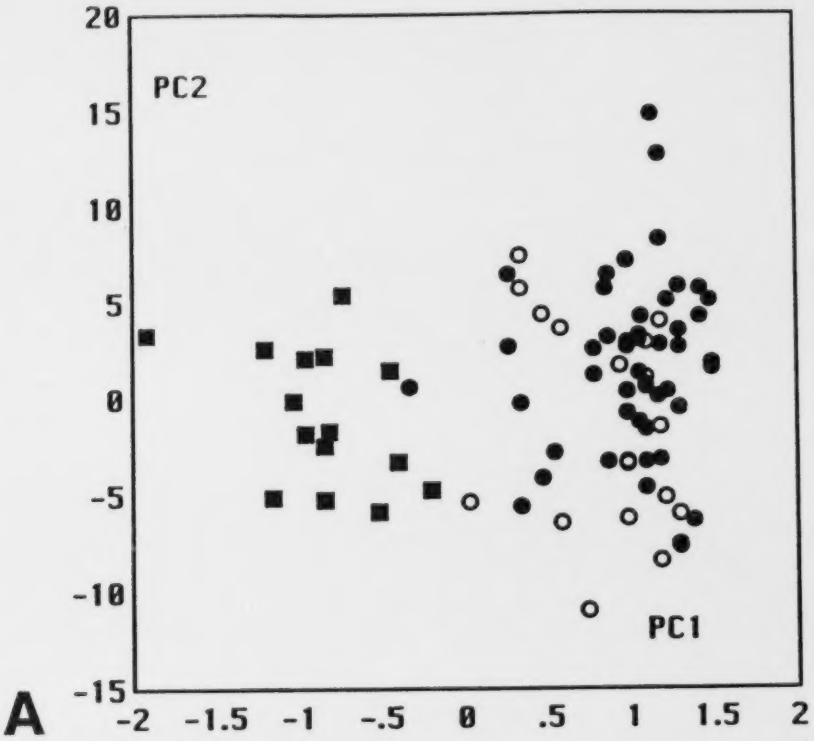
5
0
-5
-10
-15
-1.5
-1
-.5
0
.5
1
1.5

B

FIG. 8. Principal components analysis of two species of Limnichthys: L. fasciatus (solid circles; the Fijian specimens shown as open circles) and L. donaldsoni (solid square/solid triangle). A) Scatter of Component I of the meristic dataset, excluding color (PC1) andComponent II of the morphometric dataset (PC2); B) Scatter of Component I of the meristic dataset, including color (PC1) and Component II of the morphometric dataset (PC2).


PC2
PC1
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-15
-2
-1.5
-1
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0
.5
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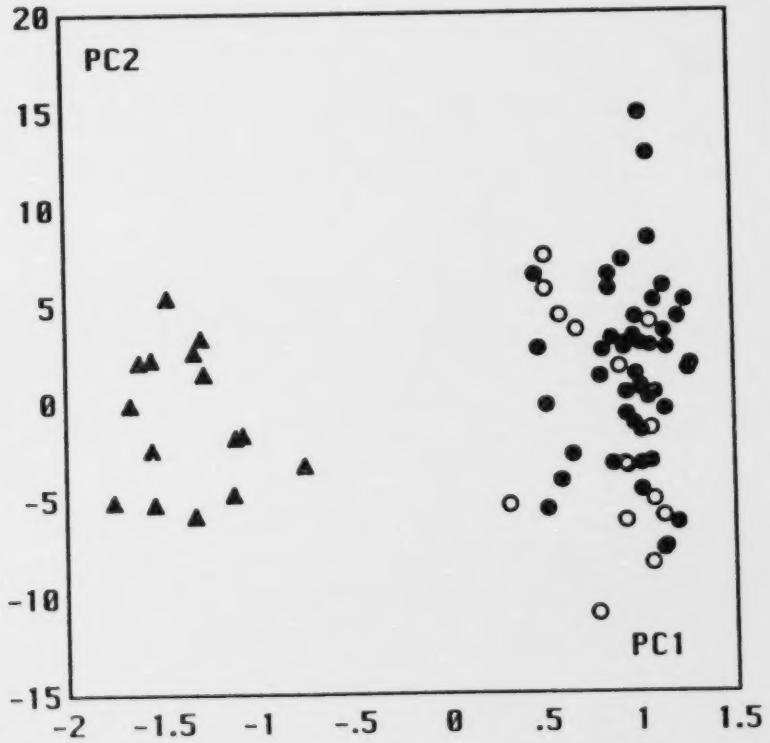
1.5
2

A


PC2
PC1
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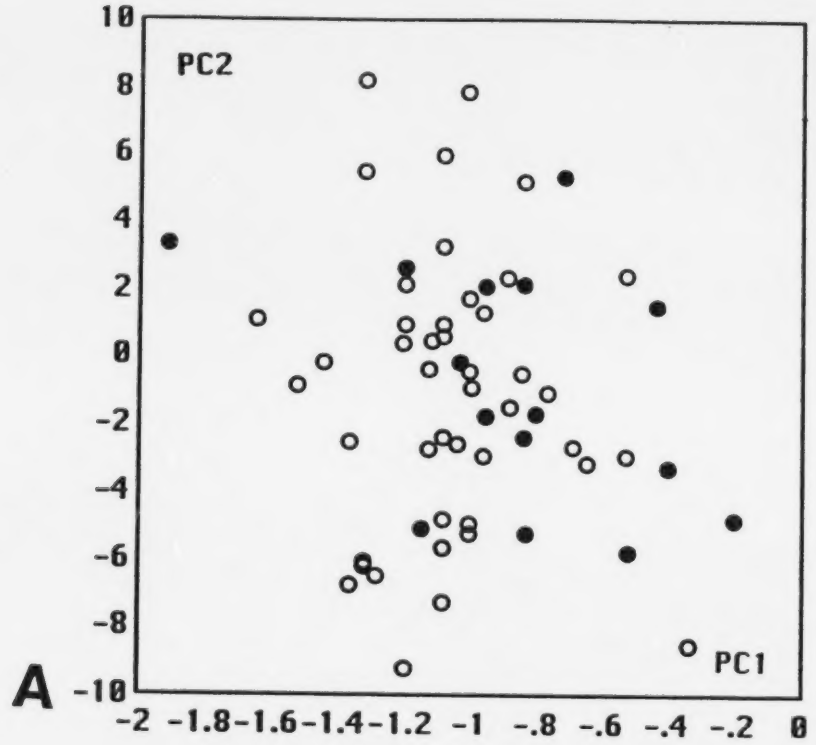
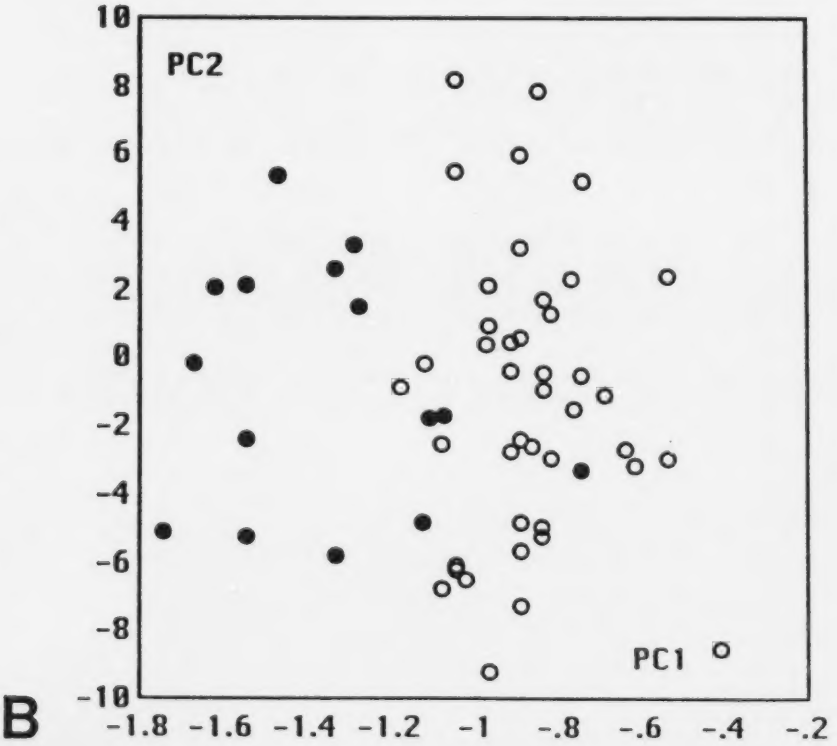
-10
-15
-2
-1.5
-1
-.5
0
.5
1
1.5

B

FIG. 9. Principal components analysis of two species of Limnichthys: L. nitidus (open circles) and L. donaldsoni (solid circle). A) Scatter of Component I of the meristic dataset, excluding color (PC1) and Component II of the morphometric dataset (PC2); B) Scatter of Component I of the meristic dataset, including color (PC1) and Component II of the morphometric dataset (PC2).


PC2
PC1
10
8
6
4
2
0
-2
-4
-6
-8
-10
-2 -1.8 -1.6 -1.4 -1.2 -1 -.8 -.6 -.4 -.2 0

A


PC2
PC1
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8
6
4
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0
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-4
-6
-8
-10
-1.8 -1.6 -1.4 -1.2 -1 -.8 -.6 -.4 -.2

B

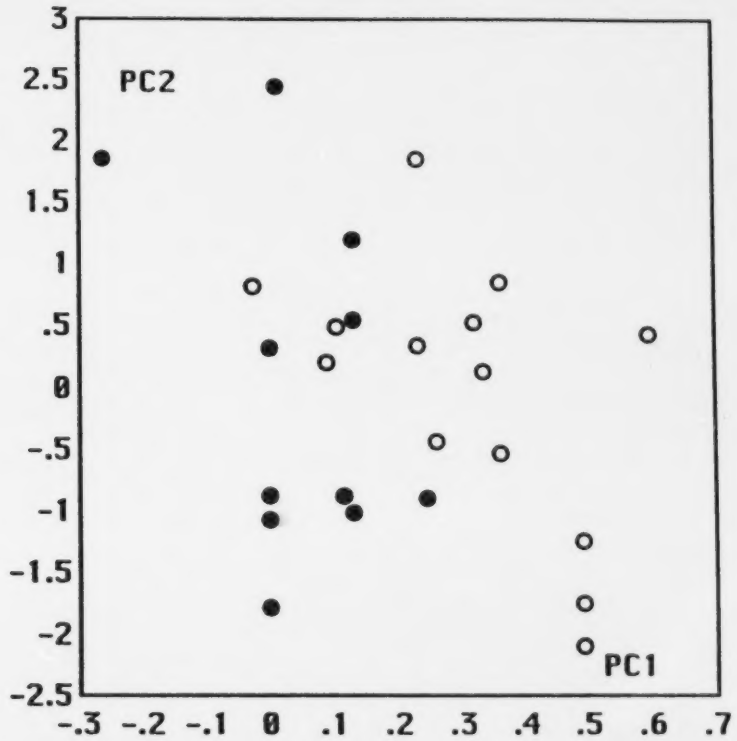
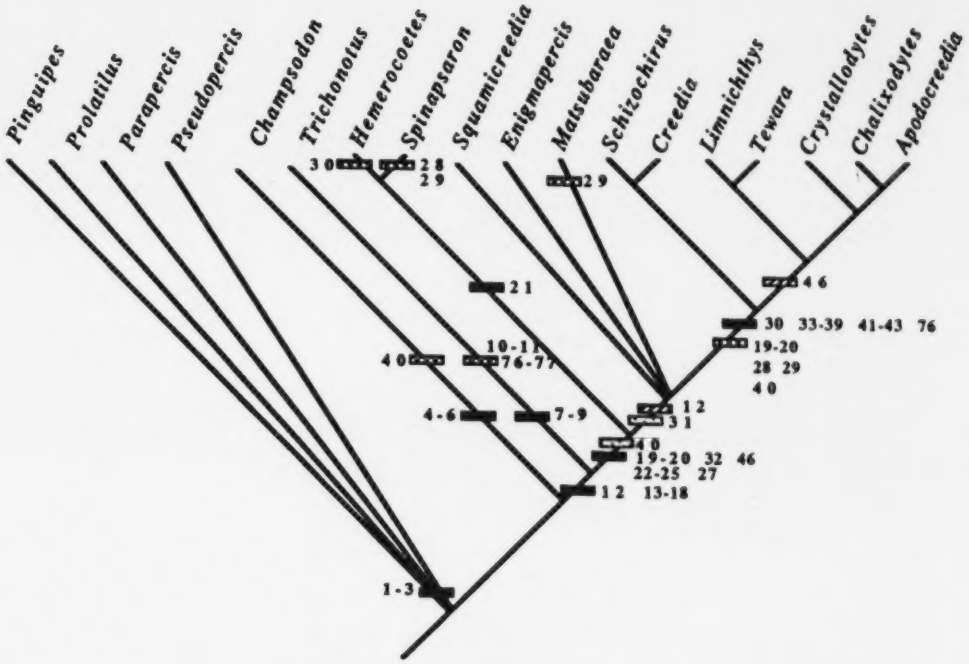


Fig. 10 Principal components analysis of the two species of Chalixodytes. C. tauensis (solid circles) and C. chamaleontoculis (open circles). Scatter of Component I of the meristic dataset (PC1) and Component II of the mophometric dataset (PC2).

FIG. 11. Minimum length cladogram obtained form PAUP. A) hypothesized relationships of the outgroup to the Creediidae; B) Creediidae node, showing proposed generic interrelationships.


Pinguipes
Prolatilus
Parapercis
Pseudopercis
Champsodon
Trichonotus
Hemerocoetes
Spinapsaron
Squamicreedia
Enigmapercis
Matsubaraea
Schizochirus
Creedia
Limnichthys
Tewara
Crystallodytes
Chalixodytes
Apodocreedia
30
28
29
29
21
10-11
40
76-77
4-6
7-9
12
31
40
19-20 32 46
22-25 27
12 13-18
1-3
46
30 33-39 41-43 76
19-20
28 29
40

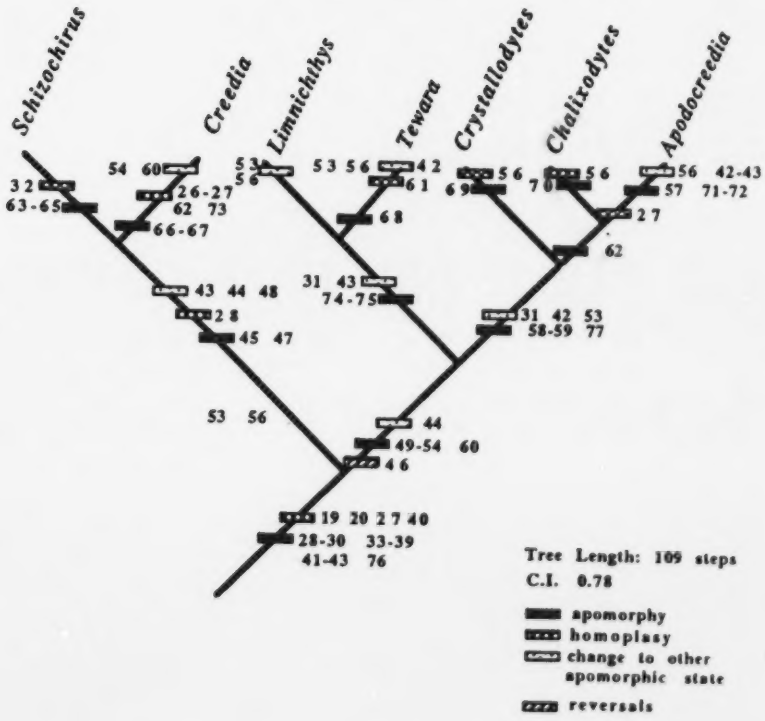

Schizochirus
Creedia
Limnichthys
Tewara
Crystallodytes
Chalixodytes
Apodocreedia
54 60
32
63-65
26-27
62 73
66-67
53
56
53 56
42
61
68
56
69
56
70
56
56 42-43
57 71-72
27
62
43 44 48
28
45 47
31 43
74-75
31 42 53
58-59 77
53 56
44
49-54 60
46
19 20 27 40
28-30 33-39
41-43 76
Tree Length: 109 steps
C.I. 0.78
apomorphy
homoplasy
change to other apomorphic state
reversals

FIG. 12. Lateral view of entire skeleton of Limnichthys fasciatus. Bar = 1mm.

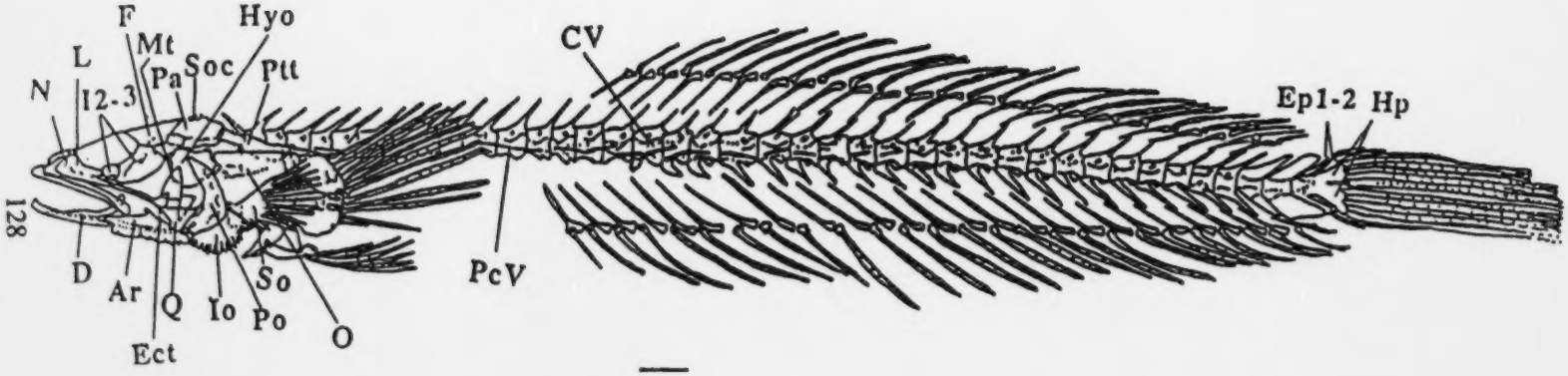
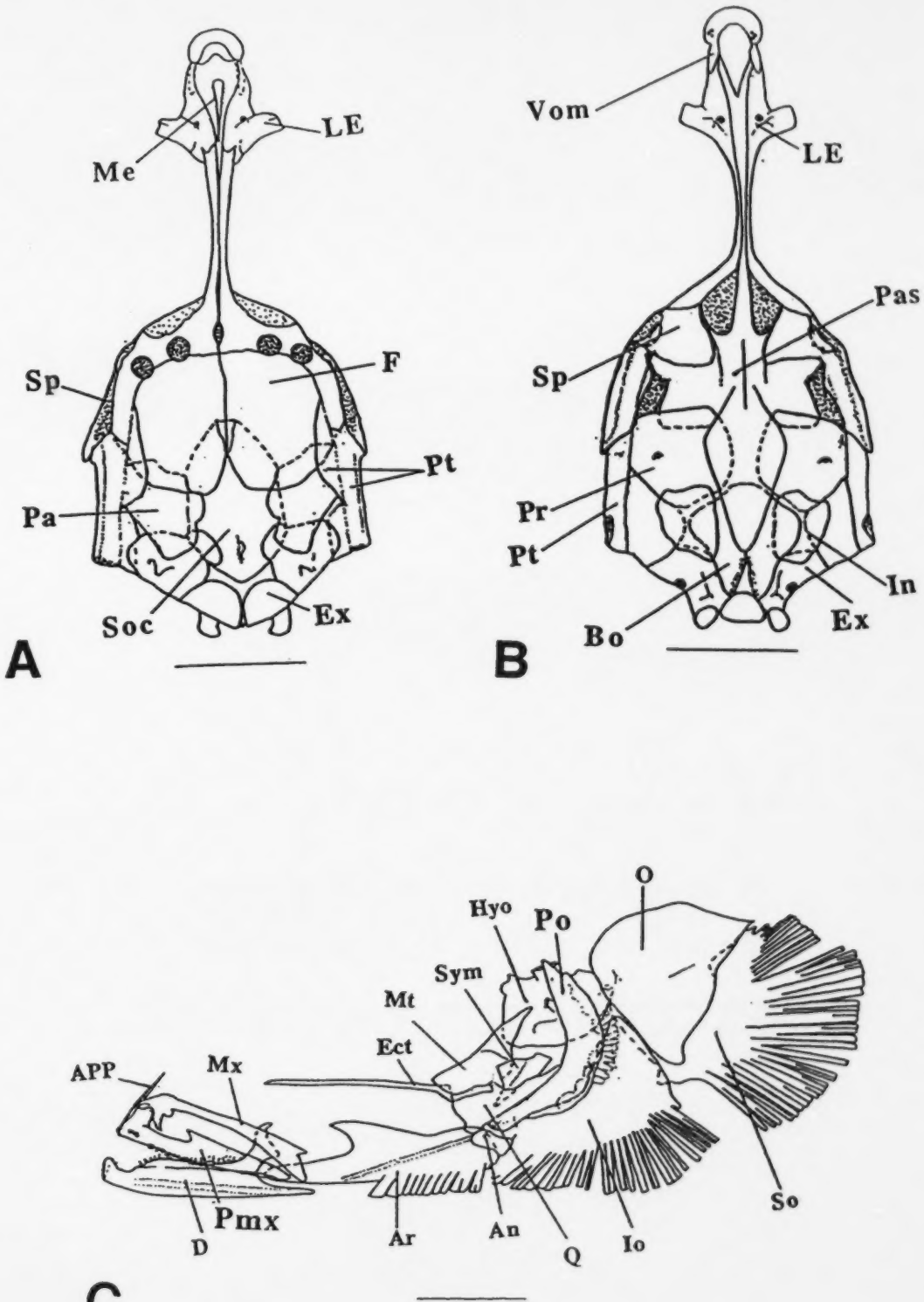

F
Hyo
Mt
L
Soc
Pa
Ptt
N
12-3
CV
Ep1-2
Hp
D
Ar
Q
Io
So
Po
O
Ect
PcV

FIG. 13. A) Skull of Creedia haswelli, dorsal view; B) Skull of Creedia haswelli, ventral view; C) jaws, suspensorium and opercular apparatus of Creedia haswelli : left lateral view. Bar = 1mm.


Me
LE
Sp
F
Pt
Pa
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Vom
LE
Pas
Sp
Pr
Pt
In
Bo
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Sym
Mt
Ect
APP
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Pmx
D
Ar
An
Q
Io
So
C

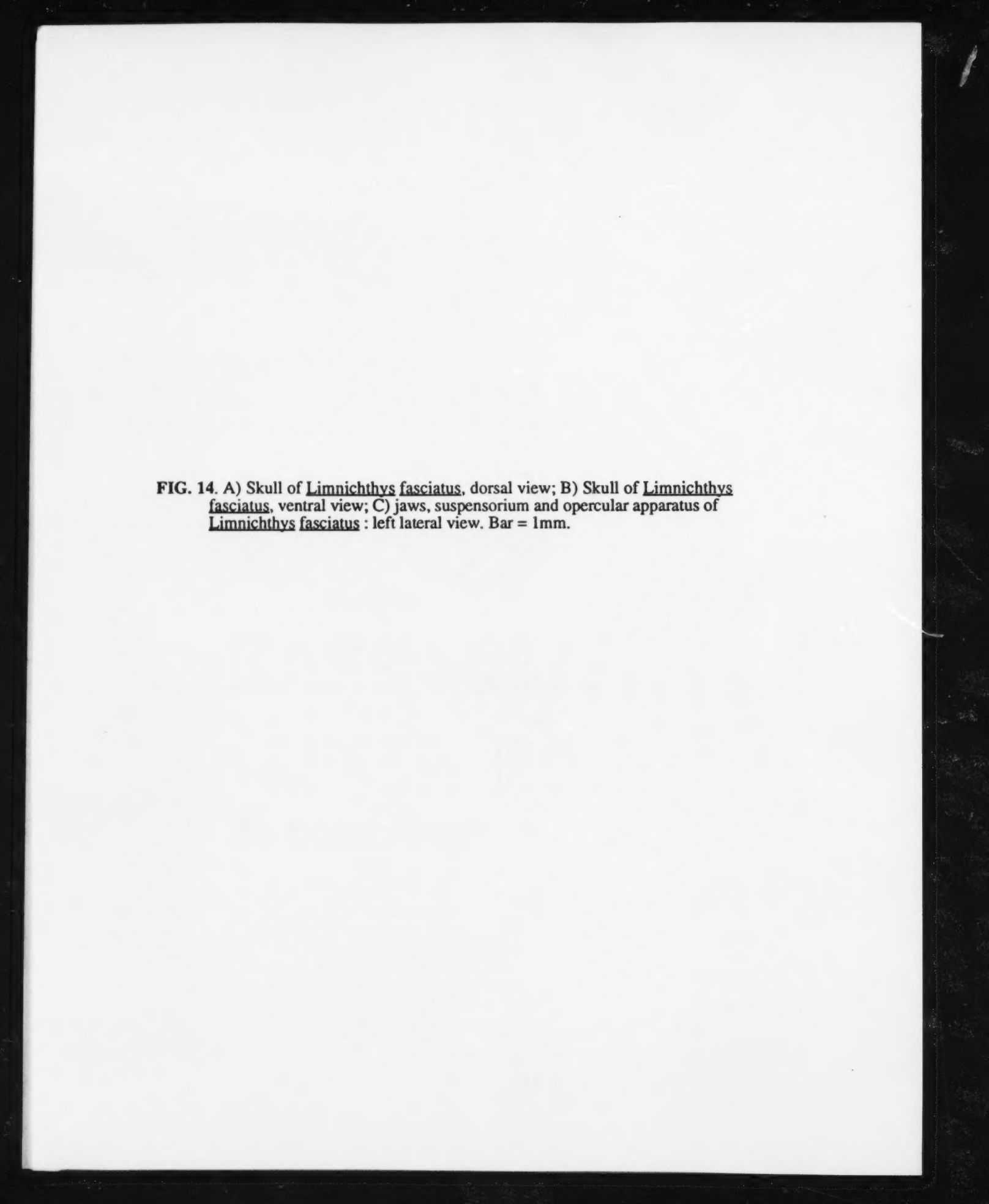
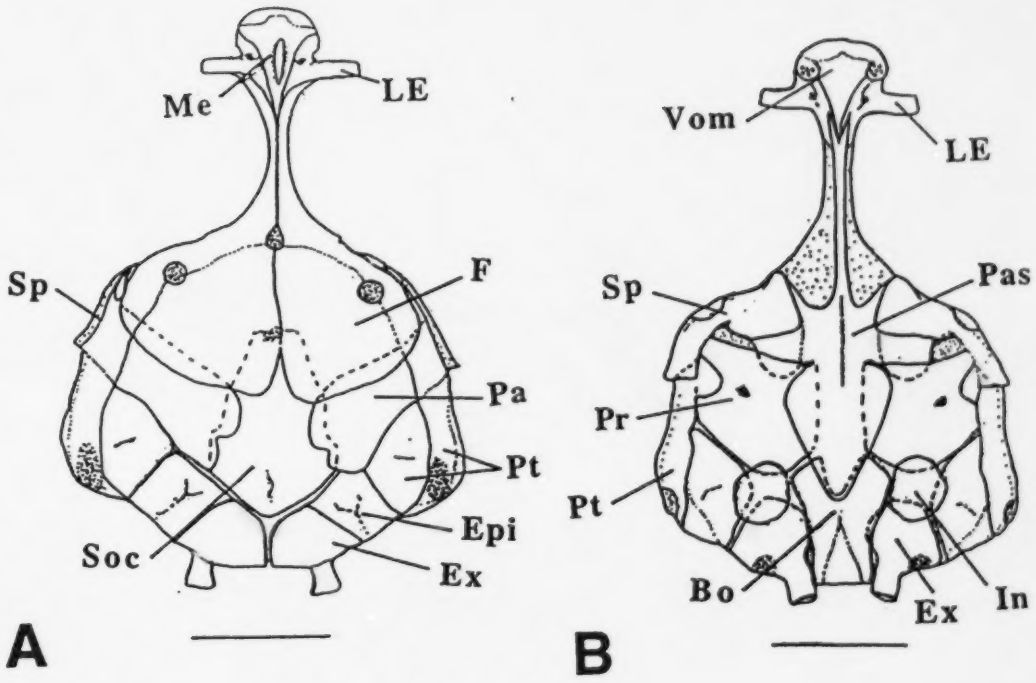


FIG. 14. A) Skull of Limnichthys fasciatus, dorsal view; B) Skull of Limnichthys fasciatus, ventral view; C) jaws, suspensorium and opercular apparatus of Limnichthys fasciatus : left lateral view. Bar = 1mm.


Me
LE
Sp
F
Pa
Pt
Epi
Soc
Ex
A
Vom
LE
Sp
Pas
Pr
Pt
Bo
Ex
In
B

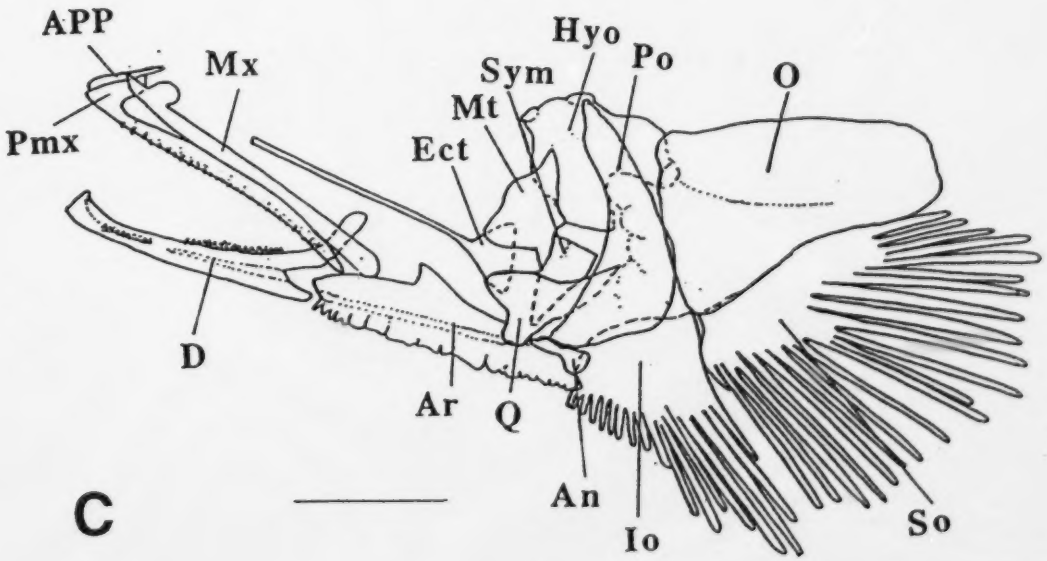
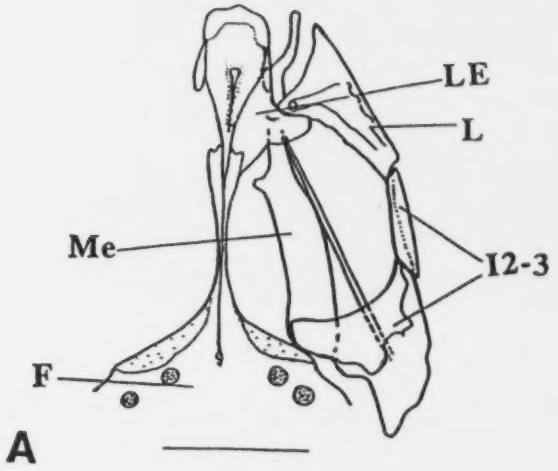
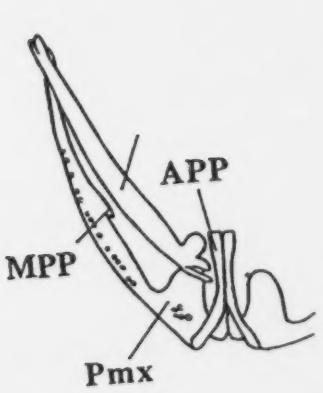

APP
Mx
Pmx
Hyo
Sym
Po
O
Mt
Ect
D
Ar
Q
An
Io
So
C

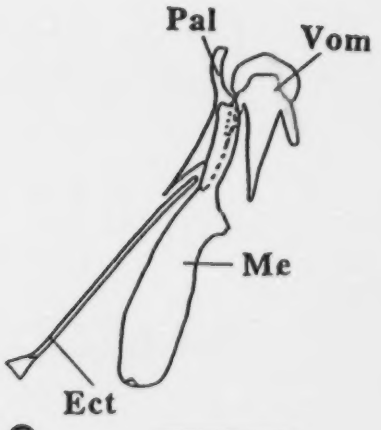
FIG. 15. A) Dorsal view of anterior region of skull of Creedia haswelli, showing infraorbital series and mesopterygoid position; B) Upper jaw of Creedia haswelli, dorsal view; C) detail of the vomer and some bones of the suspensorium of Creedia haswelli, dorsal view. Bar = 1mm.



A

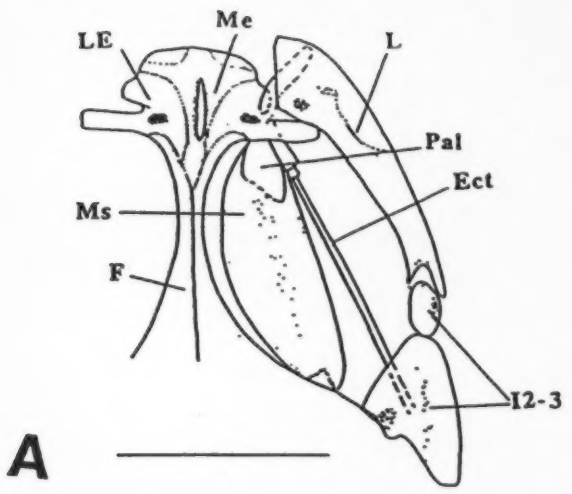


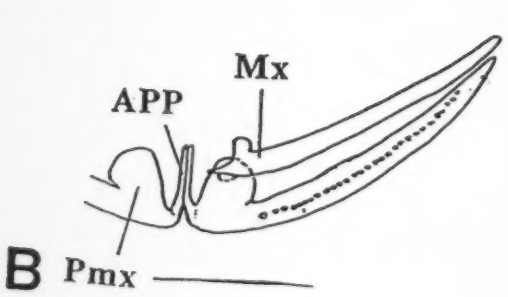
B



C

FIG. 16. A) Dorsal view of anterior region of skull of Limnichthys fasciatus, showing infraorbital series and mesopterygoid position; B) Upper jaw of Limnichthys fasciatus, dorsal view; C) detail of the vomer and some bones of the suspensorium of Limnichthys fasciatus, dorsal view. Bar = 1mm.


LE
Me
L
Pal
Ect
Ms
F
I2-3
A


APP
Mx
B
Pmx

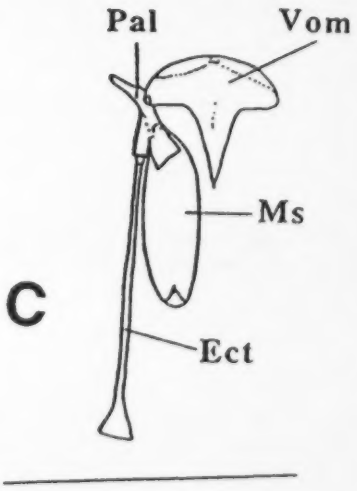
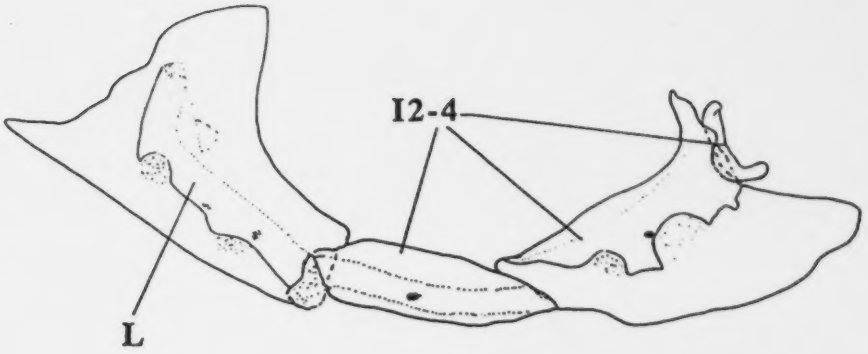
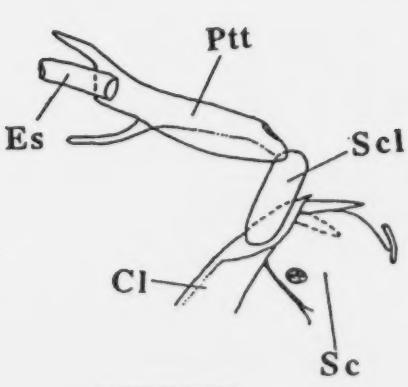

Pal
Vom
Ms
C
Ect

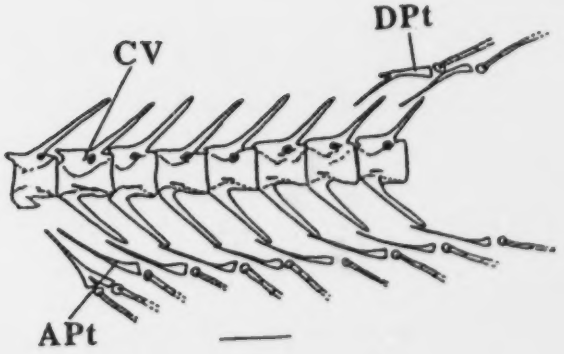
FIG. 17. A) Left lateral view of the infraorbital series of C. haswelli; B) Part of the pectoral girdle of C. haswelli, lateral view; C) Part of the axial skeleton of C. haswelli, lateral view. Bar = 1mm.



A

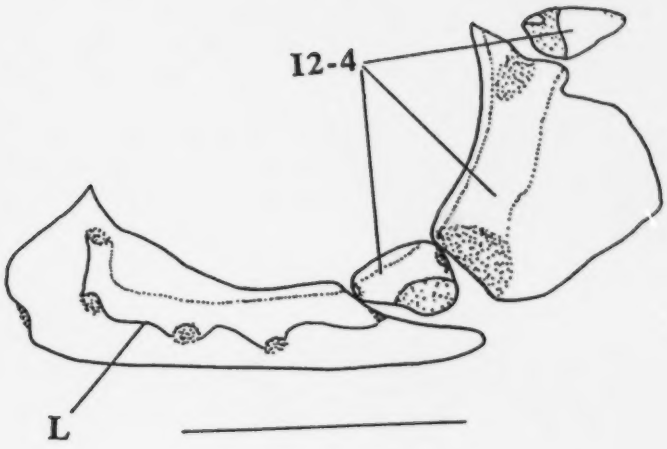


B

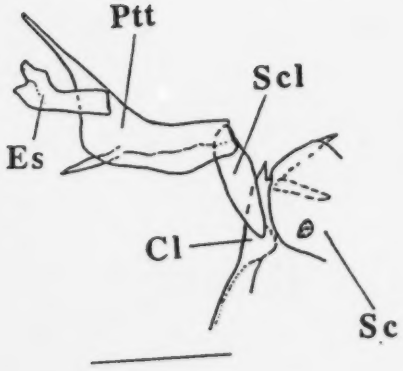


C

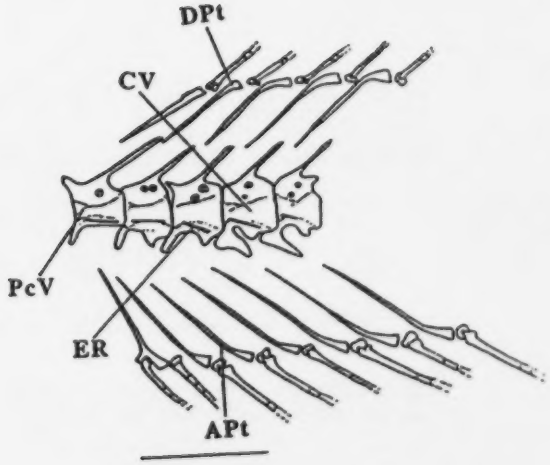
FIG. 18. A) Left lateral view of the infraorbital series of Limnichthys fasciatus B) Part of the pectoral girdle of Limnichthys fasciatus, lateral view; C) Part of the axial skeleton of Limnichthys fasciatus, lateral view. Bar = 1mm.



A

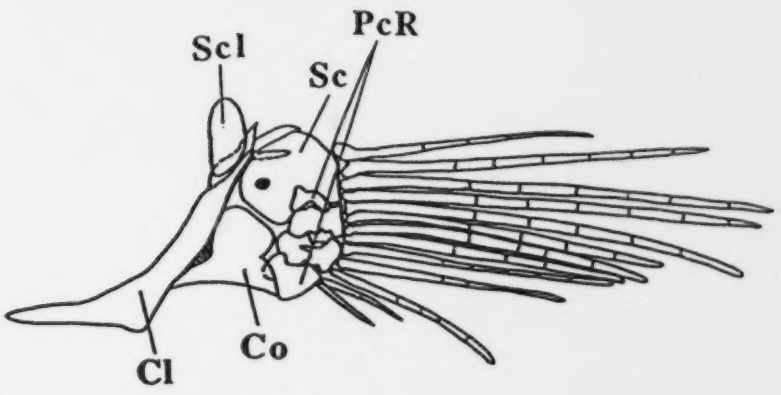


B

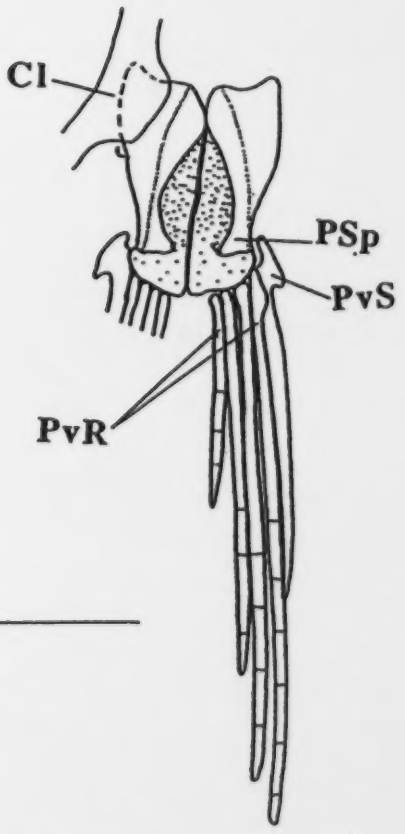


C

FIG. 19. A) Pectoral skeleton of Creedia haswelli, lateral view; B) Pelvic skeleton of Creedia haswelli, ventral view. Bar = 1mm.



A



B

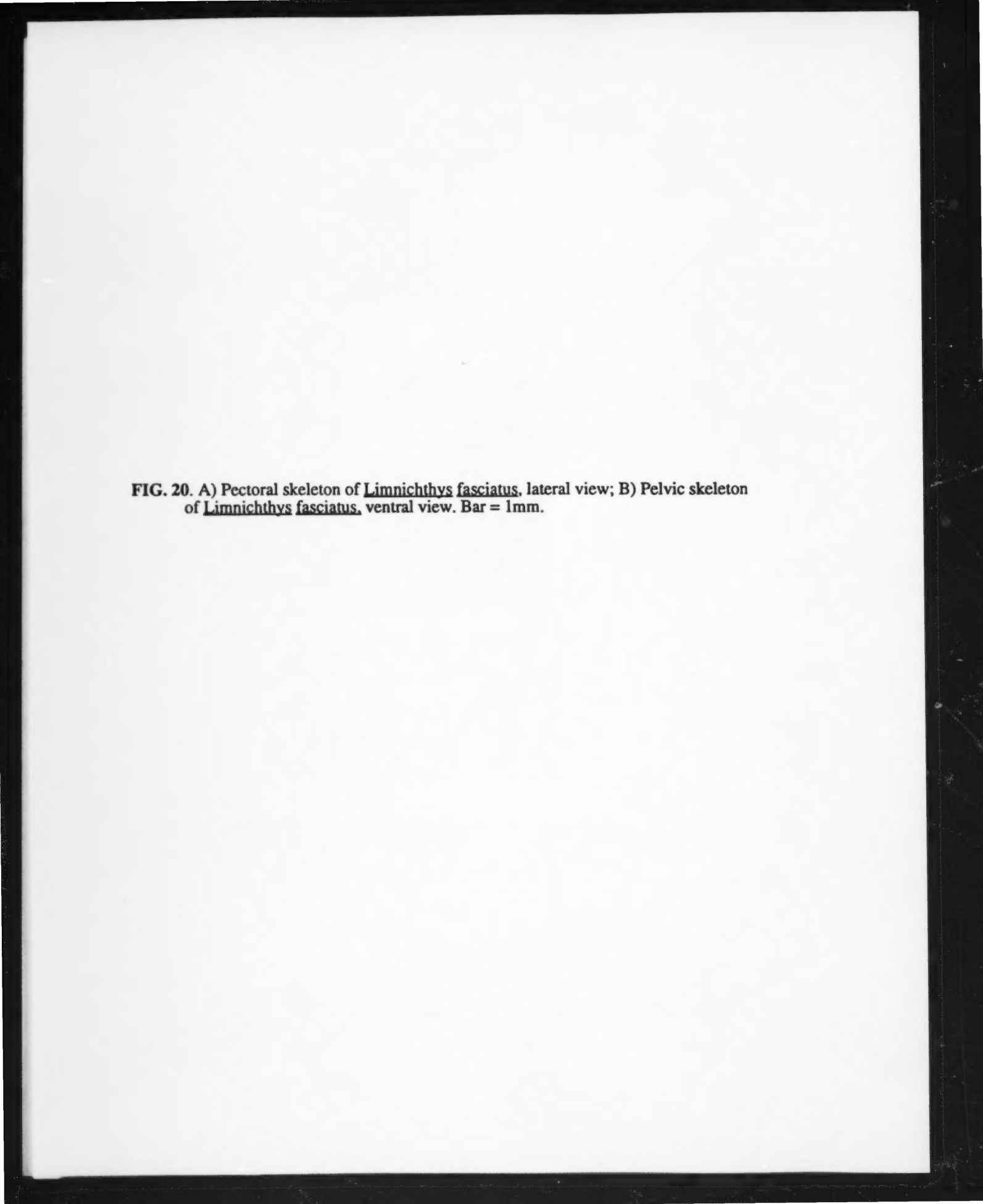
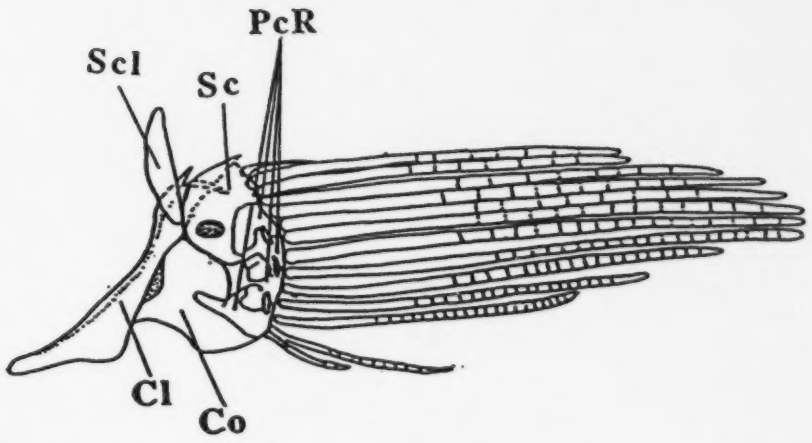
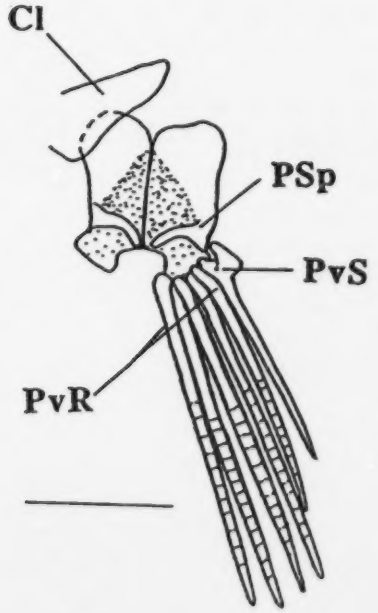


FIG. 20. A) Pectoral skeleton of Limnichthys fasciatus, lateral view; B) Pelvic skeleton of Limnichthys fasciatus, ventral view. Bar = 1mm.

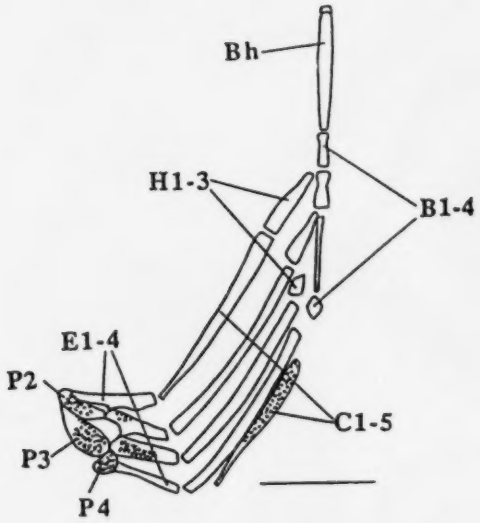


A



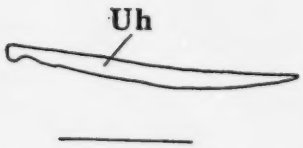
B

FIG. 21. A) Branchial arches of Creedia haswelli, left side, dorsal view of ventral surface. Epibranchials and pharyngobranchials unfolded and shown in ventral view; B) Diagrammatic representation of anterior end of urohyal of Creedia haswelli, showing its position with respect to basibranchial 2; C) Urohyal of Creedia haswelli, lateral view; D) Diagrammatic representation of the hyoid apparatus of Creedia haswelli, lateral view. Bar = 1mm.

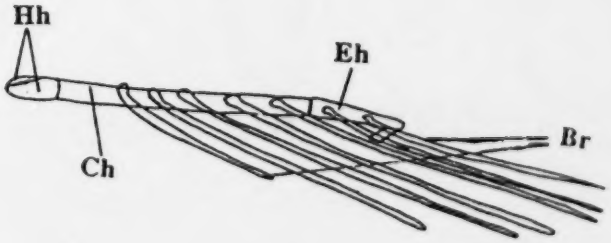


A

B

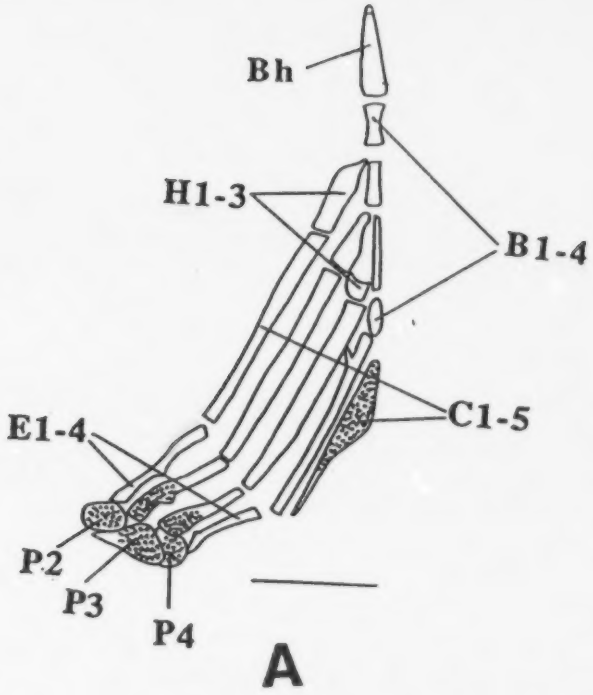


C



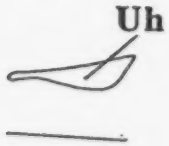
D

FIG. 22. A) Branchial arches of Limnichthys fasciatus, left side, dorsal view of ventral surface. Epibranchials and pharyngobranchials unfolded and shown in ventral view; B) Diagrammatic representation of anterior end of urohyal of Limnichthys fasciatus, showing its position with respect to basibranchial 2; C) Urohyal of Limnichthys fasciatus, lateral view; D) Diagrammatic representation of the hyoid apparatus of Limnichthys fasciatus, lateral view. Bar = 1mm

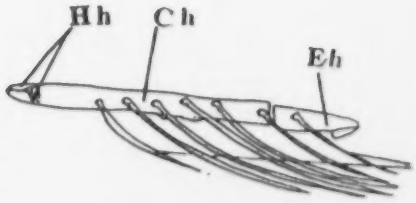


A

B



C



D

FIG. 23. A) Caudal skeleton of Creedia haswelli; B) Dorsal pterygiophore of Creedia haswelli; C) Anal pterygiophore of Creedia haswelli.

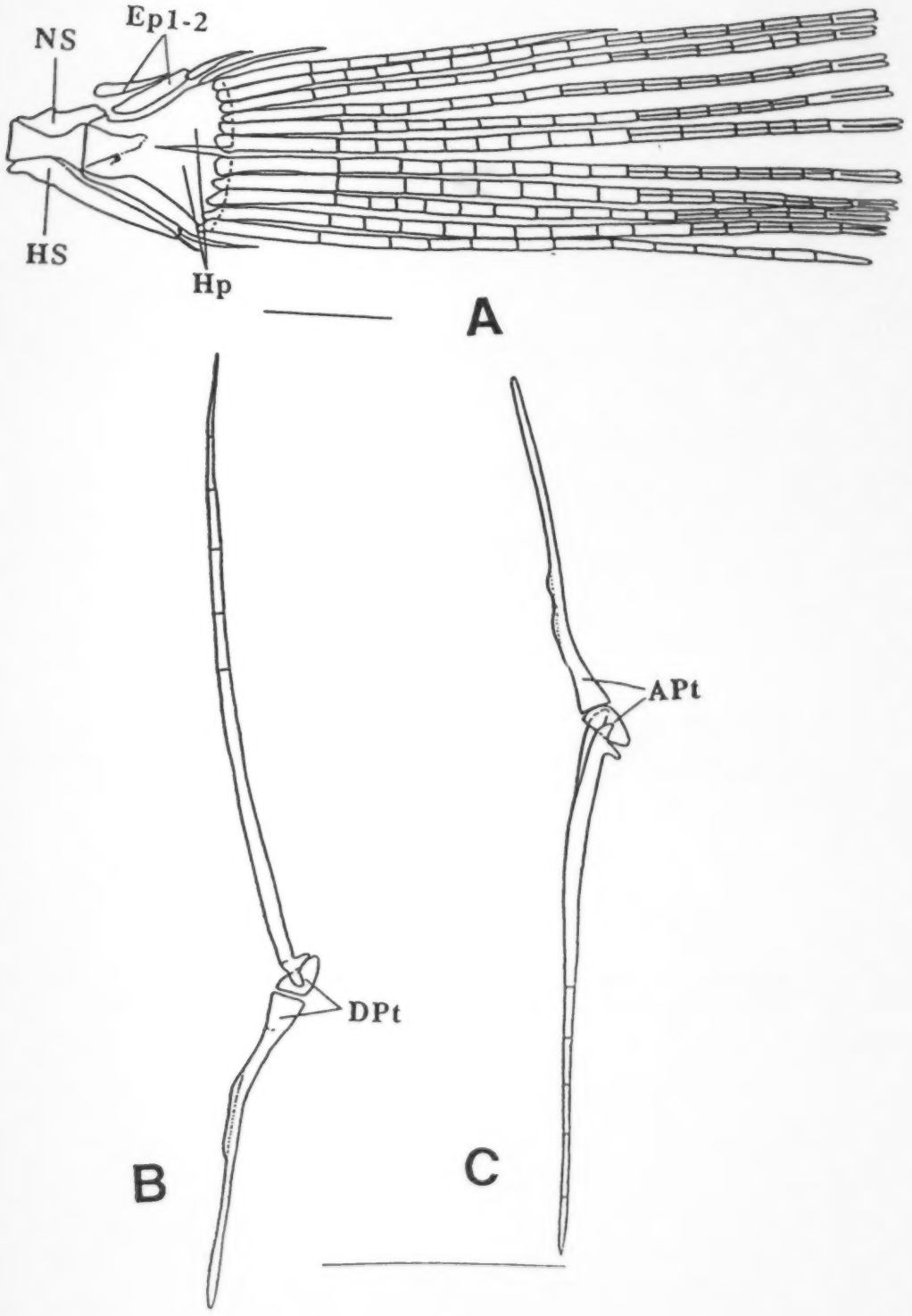
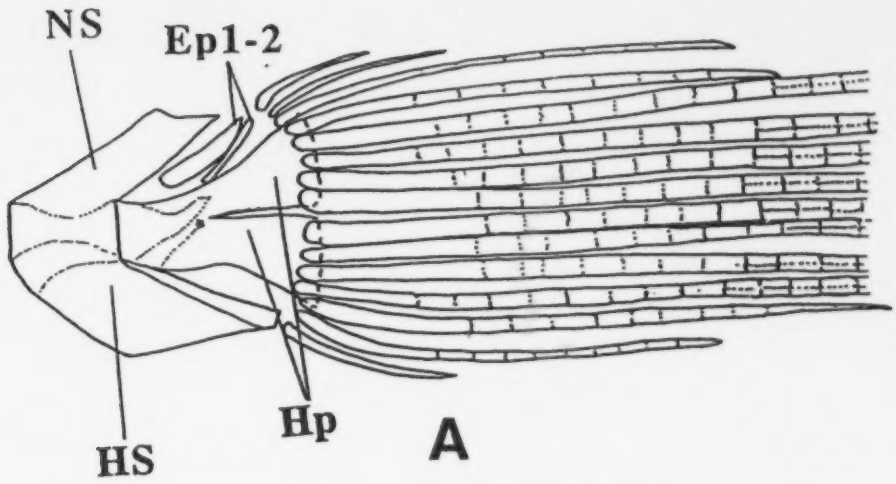

NS
Ep1-2
HS
Hp
A
APt
DPt
B
C

FIG. 24. A) Caudal skeleton of Limnichthys fasciatus; B) Dorsal pterygiophore of Limnichthys fasciatus; C) Anal pterygiophore of Limnichthys fasciatus. Bar = 1mm.


NS
Ep1-2
HS
Hp
A

DPt
B

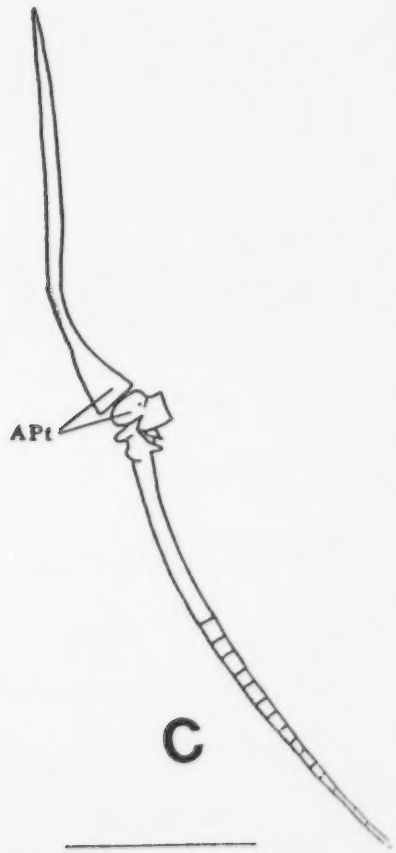

APt
C

TABLE 1. VARIOUS CLASSIFICATIONS PROPOSED FOR CREEDIIDS

Author	Suprafamiliar taxa	Suprageneric taxa	Genera
Regan (1913)	O. Percomorphii Div. Trachniformes	Fam. Creediidae Fam. Limnichthyidae	Creedia Limnichthys
Jordan (1923)	O. Jugulares	Fam. Creediidae Fam. Limnichthyidae	Creedia Limnichthys Schizochirus
McCuloch (1929)	O. Jugulares	Fam. Creediidae Fam. Limnichthyidae	Creedia Squamicreedia Limnichthys Schizochirus
Berg (1940)	O. Perciformes	Fam. Creediidae Fam. Limnichthyidae	Creedia Limnichthys Schizochirus
Schultz (1943)	O. Jugulares	Fam. Trichonotidae Subfam. Limnichthyinae	Limnichthys Schizochirus Chalixodytes Crystallodytes Tewara Creedia and five other genera
Schultz in Schultz et al. (1960)		Fam. Trichonotidae	Limnichthys Schizochirus Creedia Chalixodytes Crystallodytes Apocreedia (sic) and six other genera
Greenwood et al. (1966)	O. Perciformes S.O. Trachinoidei	Fam. Creediidae Fam. Limnichthyidae	
Nelson (1978)	I.O. Trachinoidea Chalixodytes	Fam. Creediidae Tewara Crystallodytes	Apodocreedia Creedia Limnichthys Schizochirus Squamicreedia
Nelson (1984)	O. Perciformes S.O. Trachinoidei	Fam. Creediidae	same as Nelson (1978) less Squamicreedia
Nelson (1985)	S.O. Trachinoidei	Fam. Creediidae	same as Nelson (1984)
Eschmeyer(1990)	same as Nelson (1984)	same as Nelson (1984)	same as Nelson (1984)

TABLE 2. CLASSIFICATION OF THE CREEDIIDAE (FROM NELSON, 1984)

Order Perciformes

Suborder Trachinoidei

Family Creediidae

Genus Creedia

Genus Limnichthys

Genus Schizochirus

Genus Tewara

Genus Chalixodytes

Genus Crystallodytes

Genus Apodocreedia

TABLE 3 .- FREQUENCY DISTRIBUTION OF NUMBER OF DORSAL FIN RAYS OF THE 14 SPECIES OF CREEDIIDAE

SPECIES	NUMBER OF DORSAL FIN RAYS																										MEAN
	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	
Schizochirus insolens								3																							19.0
Creedia haswelli	8	24	29	3	18																										13.9
Creedia alleni	1	2																													12.6
Creedia partimsquamigera			1	1																											14.5
Creedia bilineatus					1																										–
Limnichthys fasciatus										2	6	14	24	25	10	7	1														24.1
Limnichthys nitidus									1	25	53	34	3																		22.1
Limnichthys polyactis																		11	33	8	2	1									30.6
Limnichthys rendahli																			30	4	2										30.6
Tewara cranwellae																							14	41	9						34.9
Crystallodytes cookei																									13	21	17	4			37.2
Crystallodytes pauciradiatus																			1	–	1										31.0
Chalixodytes tauensis																								1	19	10	17	5	3	1	36.7
Apodocreedia vanderhorsti																								10	31	39	10	10	8		37.0

TABLE 4 .- FREQUENCY DISTRIBUTION OF NUMBER OF ANAL FIN RAYS OF THE 14 SPECIES OF CREEDIIDAE

SPECIES	ANAL FIN RAYS																						MEAN
	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
Schizochirus insolens											1	2												28.6
Creedia haswelli					1	2	43	25	10															24.2
Creedia alleni						1	1																	23.5
Creedia partimsquamigera									1	1														26.5
Creedia bilineatus	1																							–
Limnichthys fasciatus							3	10	9	30	32	5												27.0
Limnichthys nitidus					1	9	33	48	19	5														24.8
Limnichthys polyactis													1	8	28	14	2							30.9
Limnichthys tendahli												1	2	5	4									31.0
Tewara cranwellae																			9	20	30	6		38.1
Crystallodytes cookei																		3	15	18	15	2	2	37.1
Crystallodytes pauciradiatus																			1	1				36.5
Chalixodytes tauensis																			11	14	18	9	5	37.7
Apodocreedia vanderhorsti															15	16	34	32	10	1				34.1

TABLE 5 .- FREQUENCY DISTRIBUTION OF NUMBER OF PECTORAL AND PELVIC FIN RAYS OF THE 14 SPECIES OF CREEDIIDAE

SPECIES	PECTORAL FIN RAYS						MEAN	PELVIC FIN RAYS			MEAN
	11	12	13	14	15	16		3	4	5	
Schizochirus insolens						3	16.0			3	5
Creedia haswelli	20	43	19				11.9		82		4
Creedia alleni		2	1				12.3	3			3
Creedia partimsquamigera			2				13.0		2		4
Creedia bilineatus	1						11.0	1			3
Limnichthys fasciatus	1	34	49	5			12.6			89	5
Limnichthys nitidus	3	35	64	14			12.7			116	5
Limnichthys polyactis		5	30	16	3		13.3			54	5
Limnichthys rendahli				7	5		14.4			12	5
Tewara cranwellae			36	28			13.4			64	5
Crystallodytes cookei		31	24				12.4			55	5
Crystallodytes pauciradiatus		2					12.0			2	5
Chalixodytes tauensis	22	35					11.4		57		4
Apodocreedia vanderhorsti		37	62	9			12.7	–	–	–	–

TABLE 6 .- FREQUENCY DISTRIBUTION OF NUMBER OF LATERAL LINE SCALES OF 14 SPECIES OF CREEDIIDAE.

SPECIES	LATERAL LINE SCALES																										MEAN
	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	
Schizochirus insolens			2	1																								36.3
Creedia haswelli			12	8	8	15	18	11	10																			39.1
Creedia alleni								1	1																			41.2
Creedia partimsquamigera											1	1																44.5
Creedia bilineatus	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Limnichthys fasciatus	2	-	-	8	19	29	22	7	2																			38.9
Limnichthys nitidus	10	40	28	21	11	6																						37.2
Limnichthys polyactis								3	5	11	19	10	4	2														43.8
Limnichthys rendahli						1	2	4	4	1																		41.2
Tewara cranwellae															19	24	10	10	1									49.2
Crystallodytes cookei																			22	12	15	5	-		1			54.1
Crystallodytes pauciradiatus																				1	1							54.5
Chalixodytes tauensis																				1	12	13	10	21	9	1		56.8
Apodocreedia vanderhorsti																						53	44	9	2			56.6

TABLE 7 .- Morphometrics (% SL) of Schizochirus insolens (n=3). Values for the variables marked by an asterisk were obtained from two specimens.

VARIABLES	MEAN	SD	RANGE
HL	25.3	2.0	23.0-27.6
SNL	5.9	0.8	5.2-6.8
ED	4.2	0.8	3.2-4.7
IDF	2.3	0.6	1.7-2.9
IDB	1.6	0.6	0.9-2.1
POL	16.2	1.3	14.9-17.4
MXL	9.6	0.6	8.9-10.2
OPL	16.2	1.2	14.9-17.4
PDL	49.6	1.3	49.4-51.1
PAL	36.6	1.8	34.6-38.1
PCL*	17.0	0.0	17.0
PVL*	8.2	0.9	7.5-8.9
BD	13.6	1.3	12.3-15.1
CPL	6.7	0.7	6.3-7.5
DFL	44.1	1.7	42.1-45.1
AFL	59.4	2.8	56.5-62.3

TABLE 8 .- Morphometrics (% SL) of Creedia haswelli (depending on the variable, n ranges from 78 to 82)

VARIABLES	MEAN	SD	RANGE
HL	21.5	1.2	20.0-23.6
SNL	5.9	1.2	4.9-7.7
ED	3.7	0.6	3.0-4.5
IDF	1.3	0.1	1.2-1.4
IDB	0.9	0.2	0.6-1.2
POL	12.9	2.2	9.2-14.7
MXL	8.4	1.4	7.3-10.8
OPL	7.6	1.4	5.8-10.8
PDL	18.4	2.8	15.8-21.4
PAL	15.1	4.2	10.0-21.4
PCL	8.5	2.6	5.7-12.7
PVL	9.5	3.1	6.4-12.7
BD	6.2	1.2	4.4-7.6
CPL	4.5	0.7	3.7-5.4
DFL	29.0	2.5	26.2-30.5
AFL	46.6	3.6	41.3-49.8

TABLE 9 .- Morphometrics (% SL) of Creedia alleni (n=3). Values for the variables marked by an asterisk were obtained from two specimens; those marked by two asteriks were obtained from one specimen.

VARIABLES	MEAN	SD	RANGE
HL	21.4	0.7	20.9-22.3
SNL	5.6	0.7	4.7-6.1
ED	3.3	0.3	3.0-3.6
IDF	1.2	0.2	0.9-1.5
IDB	0.8	0.3	0.6-1.2
POL	13.7	0.5	13.4-14.4
MXL	7.8	0.7	7.0-8.2
OPL	7.7	1.1	6.8-9.0
PDL	60.2	2.0	58.0-61.9
PAL	45.5	2.3	43.7-48.2
PCL*	12.0	1.7	10.8-13.2
PVL**	7.3	0.0	7.3
BD	5.5	0.2	5.2-5.6
CPL	3.9	0.7	3.2-4.6
DFL*	22.7	3.5	25.2-30.2
AFL	43.6	3.7	40.9-46.2

TABLE 10 .- Morphometrics (% SL) of Creedia partimsquamigera (n=2)

VARIABLES	MEAN	SD	RANGE
HL	14.9	0.2	14.8-15.0
SNL	3.8	0.1	3.7-3.9
ED	2.1	0.4	1.8-2.4
IDF	1.1	0.1	1.0-1.2
IDB	0.5	0.1	0.5-0.6
POL	12.6	0.6	12.2-13.0
MXL	5.6	0.2	5.4-5.7
OPL	6.0	0.2	5.9-6.2
PDL	62.1	4.2	59.1-65.1
PAL	45.6	0.8	44.9-46.2
PCL	7.9	0.4	7.7-8.3
PVL	4.9	0.8	4.4-5.6
BD	6.5	0.4	6.2-6.7
CPL	3.4	0.4	3.2-3.7
DFL	32.6	1.9	31.2-34.0
AFL	54.9	7.0	49.9-59.9

TABLE 11 .- Morphometrics (% SL) of Creedia bilineatus (n=1, partially dissected cleared and stained specimen).

VARIABLES	MEAN	SD	RANGE
HL	21.2	–	–
SNL	–	–	–
ED	4.4	–	–
IDF	–	–	–
IDB	1.6	–	–
POL	–	–	–
MXL	–	–	–
OPL	5.6	–	–
PDL	60.3	–	–
PAL	60.0	–	–
PCL	18.4	–	–
PVL	6.6	–	–
BD	10.0	–	–
CPL	4.1	–	–
DFL	35.6	–	–
AFL	37.5		

TABLE 12 .- Morphometrics (% SL) of Tewara cranwellae (n=64)

VARIABLES	MEAN	SD	RANGE
HL	20.6	1.1	19.1-22.7
SNL	4.8	0.6	3.9-6.3
ED	3.1	0.6	1.6-4.1
IDF	1.4	0.3	1.1-1.8
IDB	0.9	0.2	0.6-1.4
POL	10.5	3.1	6.6-8.5
MXL	7.6	0.6	6.1-7.1
OPL	7.2	0.8	5.2-8.1
PDL	36.4	3.2	30.0-42.5
PAL	33.3	2.1	30.0-37.3
PCL	10.8	1.6	8.4-14.0
PVL	7.1	2.0	4.0-10.1
BD	9.0	0.7	7.8-10.2
CPL	4.5	0.6	3.8-6.1
DFL	60.5	3.6	54.7-67.4
AFL	64.2	2.2	60.8-67.4

TABLE 13 .- Morphometrics (% SL) of Limnichthys fasciatus (n=89)

VARIABLES	MEAN	SD	RANGE
HL	27.5	1.9	19.8-31.3
SNL	6.8	0.9	4.6-9.1
ED	4.8	1.1	3.2-8.5
IDF	2.7	0.6	1.5-3.7
IDB	1.6	0.5	0.8-3.2
POL	18.2	1.5	10.2-21.7
MXL	11.1	1.4	7.6-14.6
OPL	10.8	1.4	7.6-14.7
PDL	47.5	3.3	39.9-60.9
PAL	42.6	2.6	29.4-48.8
PCL	21.3	2.3	15.6-26.2
PVL	11.4	1.8	7.4-16.4
BD	10.5	1.3	7.3-14.2
CPL	6.3	0.7	4.9-7.9
DFL	51.9	4.3	37.9-62.3
AFL	57.17	4.3	35.8-65.9

TABLE 14 .- Morphometrics (% SL) of Limnichthys nitidus (n=116)

VARIABLES	MEAN	SD	RANGE
HL	28.1	2.6	18.9-34.9
SNL	6.4	1.7	4.6-10.5
ED	4.7	0.8	3.4-6.5
IDF	2.3	0.4	1.6-3.2
IDB	1.5	0.4	0.7-2.7
POL	18.9	1.9	13.6-26.4
MXL	11.1	1.3	8.8-14.8
OPL	10.3	1.8	7.0-18.3
PDL	49.8	2.9	42.7-61.3
PAL	45.5	2.7	39.8-50.8
PCL	17.6	2.6	12.1-23.4
PVL	10.3	1.5	6.7-13.8
BD	11.0	1.5	7.7-13.6
CPL	6.5	0.8	5.0-8.9
DFL	46.4	3.3	36.1-52.6
AFL	50.7	3.8	39.4-58.4

TABLE 15 .- Morphometrics (% SL) of Limnichthys rendahli (n=12).

VARIABLES	MEAN	SD	RANGE
HL	26.0	0.8	24.8-27.9
SNL	7.2	0.5	6.3-8.2
ED	3.9	0.4	3.4-4.7
IDF	1.7	0.1	1.5-1.8
IDB	1.0	0.1	0.7-1.2
POL	16.6	0.6	15.3-17.5
MXL	9.9	0.9	8.2-11.3
OPL	8.7	0.7	7.6-9.7
PDL	44.3	1.0	43.1-46.2
PAL	45.9	1.1	43.9-47.8
PCL	17.2	1.2	14.3-18.8
PVL	9.6	1.2	8.3-12.1
BD	10.2	0.7	8.9-11.5
CPL	6.3	0.4	5.5-6.9
DFL	53.6	2.5	47.3-56.6
AFL	54.8	1.3	52.9-56.9

TABLE 16 .- Morphometrics (% SL) of Limnichthys polyactis (n=54)

VARIABLES	MEAN	SD	RANGE
HL	26.1	2.5	22.8-36.6
SNL	5.6	0.9	4.2-10.5
ED	3.8	0.7	2.7-5.8
IDF	2.1	0.4	1.4-3.2
IDB	1.1	0.3	0.6-1.9
POL	17.6	0.8	15.6-19.6
MXL	10.7	1.2	8.2-15.1
OPL	10.0	1.0	7.8-13.8
PDL	41.6	1.9	38.1-45.9
PAL	37.9	1.8	34.3-41.8
PCL	18.1	1.5	14.1-21.1
PVL	10.5	1.4	7.5-15.3
BD	10.9	1.2	8.8-17.6
CPL	5.8	0.7	42.5-60.9
DFL	55.9	3.8	42.6-60.9
AFL	61.7	2.0	54.7-65.0

TABLE 17 .- Morphometrics (% SL) of Crystallodytes cookei (n=55)

VARIABLES	MEAN	SD	RANGE
HL	21.1	1.1	19.4-23.0
SNL	5.2	0.5	4.3-6.1
ED	3.5	0.5	2.7-4.2
IDF	1.6	0.3	1.0-2.7
IDB	0.9	0.2	0.7-1.3
POL	13.7	0.8	12.5-15.1
MXL	9.3	0.7	7.6-10.3
OPL	6.6	0.7	5.1-7.6
PDL	37.8	1.3	33.9-41.4
PAL	37.7	1.3	36.0-40.0
PCL	9.2	0.9	7.4-10.5
PVL	6.6	0.6	5.5-7.6
BD	7.9	1.0	5.7-9.3
CPL	3.3	0.3	2.6-3.9
DFL	61.8	1.8	59.0-64.4
AFL	58.6	1.4	56.6-62.1

TABLE 18 .- Morphometrics (% SL) of Crystallodytes pauciradiatus (n=2)

VARIABLES	MEAN	SD	RANGE
HL	22.6	0.6	22.2-23.0
SNL	5.9	0.2	5.7-6.1
ED	3.3	0.7	2.7-3.7
IDF	1.7	0.3	1.5-1.9
IDB	0.9	0.1	0.8-1.0
POL	13.8	0.3	13.6-14.0
MXL	9.7	0.0	9.7
OPL	6.7	0.0	6.7
PDL	39.9	2.0	38.5-41.4
PAL	39.7	0.3	39.5-40.0
PCL	9.2	1.2	8.3-10.0
PVL	7.1	0.2	6.9-7.2
BD	7.7	0.0	7.7
CPL	3.3	0.0	3.3
DFL	59.7	1.1	59.0-60.5
AFL	58.4	0.2	58.2-58.6

TABLE 19 .- Morphometrics (% SL) of Chalixodytes tauensis (n=57)

VARIABLES	MEAN	SD	RANGE
HL	21.4	1.3	18.5-24.8
SNL	5.1	0.5	4.3-6.5
ED	3.4	0.4	2.6-4.4
IDF	1.8	0.3	1.3-2.4
IDB	1.1	0.2	0.5-1.7
POL	14.3	1.4	12.1-18.0
MXL	9.19	0.8	7.7-11.2
OPL	7.4	0.9	5.0-8.9
PDL	41.6	2.6	31.2-45.0
PAL	40.2	2.3	31.2-44.0
PCL	9.6	1.1	7.2-11.6
PVL	5.3	0.8	3.8-7.2
BD	6.9	0.8	5.8-8.4
CPL	3.7	0.4	2.9-4.4
DFL	55.9	2.4	48.7-59.7
AFL	57.5	2.1	52.9-61.3

TABLE 20 .- Morphometrics (% SL) of Apodocreedia vanderhorsti (n=108)

VARIABLES	MEAN	SD	RANGE
HL	16.8	0.7	15.8-17.5
SNL	3.9	0.3	3.5-4.2
ED	2.3	0.3	1.9-2.6
IDF	1.2	0.2	0.9-1.4
IDB	0.7	0.1	0.6-0.8
POL	11.9	0.5	10.8-12.4
MXL	6.7	0.3	6.1-7.1
OPL	5.1	0.3	4.6-5.5
PDL	35.1	2.3	31.7-38.2
PAL	41.6	1.9	39.2-45.3
PCL	7.1	0.6	5.7-7.7
PVL	–	–	–
BD	6.3	0.4	5.7-6.9
CPL	2.7	0.1	2.5-3.0
DFL	61.8	1.6	59.8-64.2
AFL	57.1	5.2	53.2-69.4

TABLE 21.- DATA MATRIX USED TO CONSTRUCT THE CLADOGRAM SHOWN IN FIG. 11. PLESIOMORPHIC STATE IS CODED AS 0, UNORDERED APOMORPHIC STATES ARE CODED AS 1 - 4. 9 = MISSING DATA (CHARACTER NOT APPLICABLE TO TAXON).

[12345678901234567890123456789012345678901234567890123456789012345678901234567]

Pinguipes
11100000000000000000000009000000000000000900000000000000000000000000000000000
Prolatilus
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Parapercis
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Pseudopercis
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Champsodon
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Trichonotus
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Hemerocoetes
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Spinopsaron
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Squamicreedia
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Enigmapercis
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Matsubaraea
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Schizochirus
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Limnichthys
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Tewara
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Creedia
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Crystallodytes
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Chalixodytes
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Apodocreedia
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APPENDIX 1. LIST OF OUTGROUP TAXA

AND

ADDITIONAL FAMILIES EXAMINED

PINGUIPEDIDAE - Pinguipes brasilianus, UW 21232 (1 C+S); Prolatilus jugularis, USNM 211454 (3 C+S); Pseudopercis semifasciata, Universidade Federal da Paraiba, uncatalogued; Parapercis kamoharai, UAMZ 5703.

CHAMPSODONTIDAE - Champsodon sp., USNM 245330 (1 C+S).

TRICHONOTIDAE - - Trichonotus sp., BPBM 27801 (2 C+S).

HEMEROCOETINAE - Matsubaraea fusiformis, CAS 32846 (1 C+S); Spinapsaron barbatus, CAS 15954 (1 C+S); Enigmapercis reducta, NMV A3811 (1 C+S, of 2); Squamicreedia sp., CSIRO 42176.01 (2 C+S, of 5); Hemerocoetes pauciradiatus, UAMZ uncatalogued.

Additional families examined:

Opistognathidae - Opistognathus maxillosus, USNM 217804 (1 C+S).

Bovichthyidae - Bovichthys variegatus, USNM 307786 (1 C+S).

Chiasmodontidae - Chiasmodon sp., USNM 254264 (2 C+S).

Malacanthidae - Malacanthus plumieri, ANSP 144222 (1 C+S).

Notograptidae - Notograptus guttatus, ANSP 109653 (2 C+S, of 15).

Nototheniidae - Notothenia nudifrons, UW 21152 (1 C+S); Trematomus loennbergii, UW 21154.

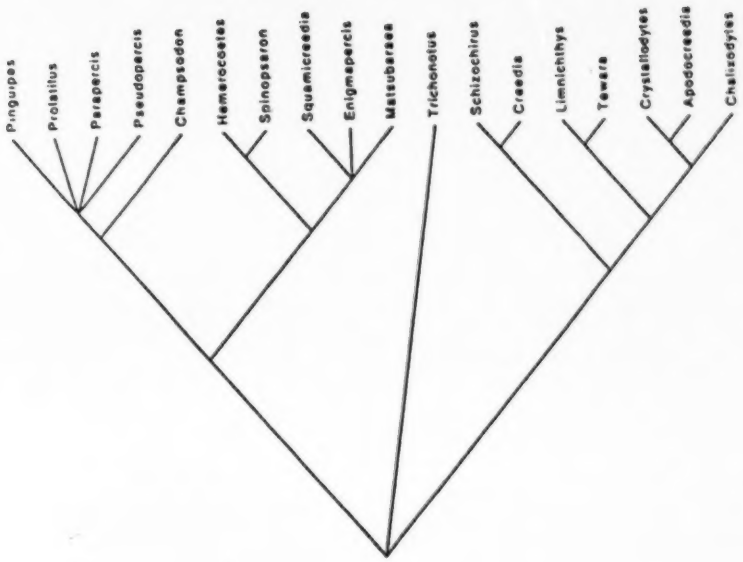
Basthymasteridae - Bathymaster signatus, UW 21157 (1 C+S).

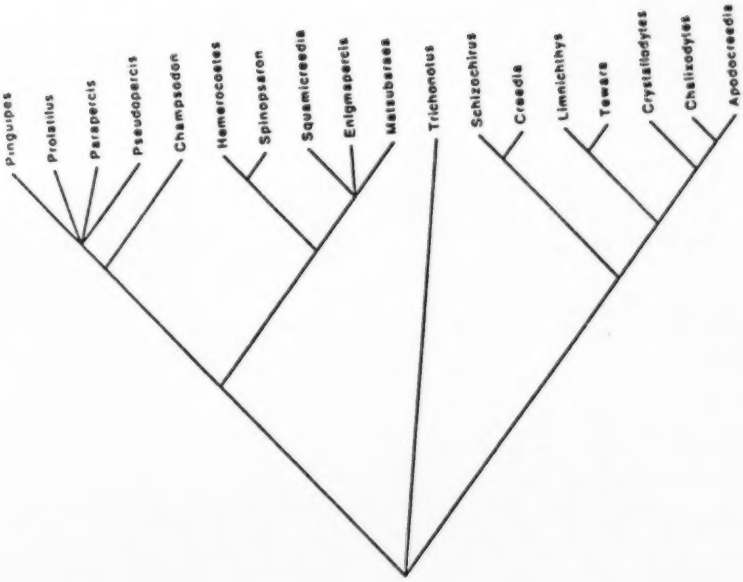
APPENDIX 2: List of characters used in the phylogenetic analysis. Character numbers correspond to those shown in Fig.11 and in Table 21. The plesiomorphic state is followed by the apomorphic states. All characters are unordered and unweighted.

1. Intercalar bone: without projection; with projection
2. Hyomandibula: without oblique crest; with crest
3. Sphenotic lateral projection: short; long
4. Nasal bone: not ridged; ridged
5. Hypurapophysis: spike-like; a rugose plate
6. Infraorbital series: with four or more bones; with three bones
7. Anterior tip of dentary: not forming a hook; forming a hook
8. Eye: without stranded lens; with stranded lens
9. lower jaw: without fleshy tip; with tip
10. lower jaw: not bordered by cirri; bordered by cirri
11. Dorsal surface of anterior tip of dentary: without knob; with knob
12. Ventral surface of anterior tip of dentary: without knob; with knob
13. Mesopterygoid: not forming floor of orbit; forming floor of orbit
14. Posterior end of dentary: not upturned; upturned
15. Ectopterygoid: widened; rod-like
16. Procurrent rays: extending onto caudal peduncle beyond epurals; not extending beyond epurals
17. Sympletic: mostly free from adjacent bones; contacting most adjacent bones
18. Opercular membranes: not extending to pectoral fin base; extending to pectoral fin base
19. Margin of maxillary process: rounded; flattened
20. First basibranchial: without lateral projections; with lateral projections
21. Maxillary spine: absent; present
22. Hypurapophysis: present; absent
23. Ribs: pleural and epipleural; epipleurals only
24. Branched caudal fin rays: more than nine; eight or nine
25. Dorsal surface of skull: with at least one extrascapular bone; without extrascapulars
26. Upper jaw fleshy extension: not forming an overhanging snout; forming an overhanging snout
27. Anterior tip of urohyal: entire; forked
28. Last dorsal pterygiophore: articulating with two rays; articulating with one ray
29. Last anal pterygiophore: articulating with two rays; articulating with one ray
30. Dorsal fin: with spinous portion; only rays present
31. Lateral line scales posterior to pectoral fin tip: not lobed; with pointed lateral lobes; with rounded lateral lobes; lateral lobes reduced.
32. Rays on lower half of pectoral fin: not thickened; thickened
33. Pelvis: flattened; cup-shaped
34. Pupil not directed forward; pupil directed forward
35. Ventral surface of upper end of cleithrum: without a spine; with a spine
36. Gill rakers: on lower and upper limbs; only on lower limb
37. Pelvis spur: anteriorly directed; medially directed
38. Lateral line: posteriorly running on midline of body; posteriorly running near the ventral profile
39. Dentary: completely toothed; not completely toothed
40. Lower arm of posttemporal: reaching intercalar; reaching skull, but not extending to intercalar; not reaching skull
41. Ectopterygoid: without fan-shaped posterior tip; with fan-shaped tip
42. Anterior tip of urohyal: on first basibranchial; on anterior tip of basibranchial 2; on middle of basibranchial 2; on posterior tip of basibranchial 2; on anterior tip of basibranchial 3
43. Posterior portion of mesopterygoid: not reaching posterior margin of orbit; reaching posterior margin of orbit; encasing eyeball posteriorly; projected onto dorsal surface of eyeball
44. Anterior portion of premaxilla: completely toothed; with a patch of canine-like teeth; without teeth
45. Vomer: without posteroventral projection; with projection
46. Neural spine of penultimate vertebra: spike-like; stub-like
47. Anterior portion of ribs: spine-like; widened
48. Maxillary process: well developed; present as a trace; absent
49. Posterior tip of maxilla: markedly broadened; slightly broadened or tapered
50. Anterior nostril: pore-like; enclosed in a tube

51. Ventral surface of caudal vertebrae: without process; with process
52. Second infraorbital: squarish or elongate; round
53. First dorsal pterygiophore: with flange or crest; with two stubs; with one stub
54. Number of poscleithra: 2; 1; 0
55. Cleithral flange: on entire surface of bone; confined to the upper half; a rudiment on upper tip of bone
56. Ascending process of premaxillae: widely separated; almost meeting medially; meeting each other; fused
57. Pectoral radials: separated or partially overlapping each other; completely overlapping one another
58. Number of anal pterygiophores preceeding first caudal vertebra: less than ten; 10 or more
59. upper corner of hypobranchial 3: without downward projection; with projection
60. Lacrymal posteroventral projection: absent; small; elongate
61. Vomerine teeth: placed directly on head; placed on projection
62. Urohyal: short; long
63. Nasal bone: without lateral flange; with flange
64. Lacrymal: without transversal groove; with groove
65. Anal pterygiophores: without flanges; with flanges
66. Number of dorsal fin rays: 19 or higher; lower than 19
67. Cheeks: without a pocket of embeded scales; with a pocket of embeded scales
68. Central frontal pore: not larger than lateral ones; larger
69. Body scales: not confined to lateral line; confined to lateral line
70. Upper half of supracleithrum: not tapered; tapered
71. Hypural plates: completely separated; partially fused
72. Pelvic fin: present; no pelvic fin
73. Number of pelvic fin rays: 5; less than five
74. Two to six last haemal spines: spike-like; squarish
75. Two to four last neural spine: spike-like; widened at the base or squarish
76. Number of epurals: three; one or two
77. Interdigitation between anal fin pterygiophores and haemal spines: both on anterior and posterior portions of body; only posteriorly

APPENDIX 3: Two 110-step cladograms obtained from PAUP, showing the hypothesized relationships of the outgroup to the Creediidae.


Pinguipes
Prolatilus
Parapercis
Pseudopercis
Champsodon
Hemerocoetes
Spinopsaron
Squamicreadia
Enigmapercis
Matsubareas
Trichonotus
Schizochirus
Creadia
Limnichthys
Tewara
Crystallodytes
Apodocreadia
Chalixodytes


Pinguipes
Prolatilus
Parapercis
Pseudopercis
Champsodon
Hemerocoetes
Spinopsaron
Squamicreadia
Enigmapercis
Matsubareas
Trichonotus
Schizochirus
Creadia
Limnichthys
Tewara
Crystallodytes
Chalixodytes
Apodocreadia